ORIGINAL RESEARCH

TITLE: A biogeographic reversal in sexual size dimorphism along a continental temperature gradient

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KEYWORDS
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ABSTRACT

The magnitude and direction of sexual size dimorphism (SSD) varies greatly across the animal kingdom, reflecting differential selection pressures on the reproductive and/or ecological roles of males and females. If the selection pressures and constraints imposed on body size change along environmental gradients, then SSD will vary geographically in a predictable way. Here, we uncover a biogeographical reversal in SSD of lizards from Central and North America: in warm, low latitude environments, males are larger than females, but at colder, high latitudes, females are larger than males. Comparisons to expectations under a Brownian motion model of SSD evolution indicate that this pattern reflects differences in the evolutionary rates and/or trajectories of sex-specific body sizes. The SSD gradient we found is strongly related to mean annual temperature, but is independent of species richness and body size differences among species within grid cells, suggesting that the biogeography of SSD reflects gradients in sexual and/or fecundity selection, rather than intersexual niche divergence to minimize intraspecific competition. We demonstrate that the SSD gradient is driven by stronger variation in male size than in female size and is independent of clutch mass. This suggests that gradients in sexual selection and male-male competition, rather than fecundity selection to maximize reproductive output by females in seasonal environments, are predominantly responsible for the gradient.

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INTRODUCTION

Within animal species, similarly-sized males and females are the exception, not the norm (Fairbairn 2007). The direction and magnitude of this sexual size dimorphism (SSD) vary greatly across the animal kingdom; in vertebrates alone, females are larger than males (female-biased SSD) in some taxa and males are larger than females in others (male-biased SSD). For example, some female deep-sea anglerfishes (Lophiiformes) are six times larger than their conspecific males (Pietsch 2005), while male northern elephant seals (*Mirounga angustirostris*) are three times larger than females (Fairbairn 2007). SSD also varies geographically in a range of taxa, including lizards (Cox et al. 2003, 2007, Algar and López-Darias 2016), bats (Storz et al. 2001), and beetles (Stillwell et al. 2007). However, these geographical patterns are not ubiquitous. For example, Cardillo (2002) found no latitudinal trend in SSD of birds, while Blanckenhorn et al. (2006) found latitudinally structured variation in SSD for two-thirds of 96 species from a variety of taxa. Friedman and Remeš's (2016) global study of over 2000 bird species identified a weak tendency for female-biased or low male-biased SSD at high latitudes, with considerable variation across the globe in environment–SSD relationships. Together, these results hint at emergent geographical patterns in SSD, but with considerable variability among taxa and regions, highlighting how much we still do not know about how SSD varies with environmental conditions, and what processes underlie these patterns (Machado et al. 2016).

SSD arises from differing selection pressures related to the reproductive and/or ecological roles of males and females (Fairbairn 2007). It may be generated and maintained by selection on resource use and survival (viability selection), or selection on reproductive output (Fitch 1976, Shine 1978, 1994, Berry and Shine 1980, Stamps 1983, Fitch and Hillis 1984, Hedrick and Temeles 1989, Cox et al. 2003, Pincheira-Donoso and Hunt 2017). The niche divergence hypothesis posits that, when interspecific competitors are few, intraspecific competition between males and females generates disruptive selection between males and females, producing sexual size dimorphism in either direction (Schoener 1977, Slatkin 1984, Shine 1989, Dayan and Simberloff 2005, Pincheira-Donoso et al. 2009, 2018, Meiri et al. 2014). Alternatively, selection on reproductive success may take the form of fecundity or sexual selection. Fecundity selection acts on females to maximize reproductive output,

via larger clutches and/or offspring, in contrast to sexual selection which acts on mating success and viability selection which acts on survival (Pincheira-Donoso and Hunt 2017). As larger females can produce larger clutches and/or hatchlings (Meiri et al. 2012, Schwarz and Meiri 2017), strong fecundity selection could favour increases in female size, possibly leading to female-biased SSD (Shine 1988, Pincheira-Donoso and Tregenza 2011, Pincheira-Donoso and Hunt 2017). Sexual selection may act via male–male competition for mates and/or territories which favours large males, increasing male-biased SSD (Stamps 1983, Cox et al. 2003, 2007).

Fecundity, viability, and sexual selection could all produce gradients in SSD if the strength of selection varies geographically. When the breeding season is short, fecundity selection should favour larger clutches and/or offspring to maximize reproductive output during the limited reproductive season (Shine 1988, Pincheira-Donoso and Tregenza 2011). As larger females can produce larger clutches and/or hatchlings (Meiri et al. 2012), selection for increased clutch mass should lead to increased female-biased SSD in seasonal environments. The strength of sexual selection via male–male competition may also vary with climate and may depend on female reproductive strategies. If females in aseasonal environments lay many clutches throughout the year (Meiri et al. 2012, Mesquita et al. 2016), then sexual selection in males may be stronger as there are greater benefits to long-term control of high-quality territories or mates than if reproduction occurs in a short burst (Machado et al. 2016). Strong fecundity selection for large females and/or weak sexual selection for large males in seasonal environments predict a gradient in SSD from male-biased SSD to female-biased SSD as seasonality increases. We refer to this as the ‘reproductive selection hypothesis’.

The niche divergence hypothesis, which relies on disruptive selection between males and females, also predicts geographical variation in SSD, but as a function of the strength of intraspecific versus interspecific competition in an area, rather than climate directly. Specifically, when the number of competitor species is high, SSD will be low as there is limited opportunity of inter-sexual divergence as resources are already exploited by competitors; alternatively, when interspecific competitors are few, there is opportunity for male and female body sizes to diverge to reduce intraspecific competition

(Schoener 1977, Slatkin 1984, Shine 1989, Dayan and Simberloff 2005, Pincheira-Donoso et al. 2009, c.f. Meiri et al. 2014). The niche divergence hypothesis predicts a negative correlation between the magnitude of SSD, regardless of whether males or females are larger, and the number of co-occurring competitor species. There is conflicting evidence for the niche divergence hypothesis. For example, Pincheira-Donoso et al. (2018) found the predicted negative relationship in local assemblages of South American *Liolaemus* lizards, but Meiri et al. (2014) found no such relationship on islands worldwide, suggesting that the signal of niche divergence on SSD is scale-dependent (De Lisle and Rowe 2015). It could also be that the number of co-occurring species is a poor proxy for competitive environment (Meiri et al. 2014). Thus, we also test whether absolute SSD relates to the spacing between adjacent species in body-size space. When species are more similar in size, there should be less potential for size divergence among the sexes (Supplementary material Appendix 1 Fig. A1).

We test for a biogeographical gradient in sexual size dimorphism for lizards across Central and North America, from southern Panama to the northern limit of lizards' ranges in southern Canada. We test predictions of the reproductive selection hypotheses by evaluating the relationships between SSD, male and female size, clutch size and climate. We test the niche divergence hypothesis by examining the relationship between the magnitude of SSD, species richness, and species packing (spacing of neighbours in body size space). To address the potential scale dependence of the SSD–species richness relationship, we carry out our tests at three different sampling grains, with the expectation that patterns should emerge most strongly at finer grain sizes, that may better reflect the existence of sympatric competing species. At large grain sizes, estimates of species richness may not reflect sympatry at local scales and thus may not accurately capture the number of competing species. This may especially be a problem in mountainous areas, which have high beta-diversity (Mena and Vázquez-Domínguez 2005). To account for this, we test whether the slope of the SSD–richness relationship is shallower in mountainous areas. We focus on lizards because their SSD ranges from female- to male-biased (Fitch 1981, Cox et al. 2007) and their ecology and life history is strongly linked to temperature (Pianka and Vitt 2003, Meiri et al. 2013). Furthermore, males of many lizard species compete for mates and territories (Stamps 1983), their morphology (including size) has been

linked to resource use, competition intensity, clutch size and reproductive output (Butler et al. 2000, Meiri 2008, Losos 2009, Meiri et al. 2012, Mesquita et al. 2016), they display a strong species richness gradient in North America (Currie 1991, Olalla-Tarraga et al. 2006, Roll et al. 2017).

METHODS

Species Data

We quantified presence-absence and species richness (SR) in 50km x 50km, 100km x 100km and 200km×200km grid cells across North and Central America using the Global Assessment of Reptile Distributions range maps (Roll et al. 2017) for all 606 lizard species inhabiting this region. We excluded cells with less than 50% land area, leaving 3521, 928 and 246 cells, respectively, for subsequent analysis. We used the maximum recorded snout–vent length (SVL) of males and females as our measure of body size for each sex from Meiri (2018). Male and female body size data were available for 446 species. We used male and female SVL to calculate sexual size dimorphism (SSD) for each species, following Cox et al. (2003):

$$SSD = \begin{cases} \dfrac{SVL_f}{SVL_m} - 1, & \text{if } SVL_f \geq SVL_m \\ -\left(\dfrac{SVL_m}{SVL_f} - 1\right), & \text{if } SVL_m > SVL_f \end{cases}$$

where SVL_f and SVL_m are female and male SVL respectively. Sexual size dimorphism is positive when females are larger than males, negative when males are larger than females, and zero when the sexes are the same size. This measure of SSD is symmetric around zero, does not asymptote, and contains information on direction, giving it desirable properties as a measure of SSD (Lovich and Gibbons 1992). To test the niche divergence hypothesis, we calculated the absolute value of SSD for each species and found the average in each grid cell. Absolute SSD measures the magnitude of SSD in a grid cell, regardless of its direction (i.e. whether SSD is male- or female-biased). We also calculated a measure of species packing by computing the mean ratio of SVL between adjacent species in SVL space (henceforth 'SVL spacing') using the mean of maximum male and female SVL

for each species (see Fig. A1). We obtained clutch mass estimates for 135 species from Meiri et al.'s (2018) database by multiplying clutch size by the mass of neonates/hatchlings (derived from their SVL using conversion equations from Feldman et al. 2016). We log-transformed clutch mass to help meet subsequent regression assumptions (see below) and calculated the mean log clutch mass in each grid cell.

Climate and Elevation Data

We used the 30 arc-second WorldClim dataset (Hijmans et al. 2005) to quantify climatic variation across North and Central America. For each grid cell we extracted the average mean annual temperature, temperature seasonality, mean annual precipitation, and precipitation seasonality. Temperature seasonality is the standard deviation of mean monthly temperatures ('BIO4' in Hijmans et al. 2005). Precipitation seasonality is the coefficient of variation of monthly precipitation ('BIO15' in Hijmans et al. 2005). The duration of conditions favourable for reproduction is likely correlated with mean climatic conditions (Meiri et al. 2012, Machado et al. 2016), for example the annual growing degrees days (sum of temperatures above 5ºC) variable from the ENVIREM dataset (Title and Bemmels 2018) had a Pearson's correlation of 0.99 with mean annual temperature in 100km x 100km grid cells. We used the global 30 arc-second elevation dataset available from Worldclim to calculate elevational range within each grid cell.

Regression Analyses

We fit a series of weighted regression models to test our hypotheses' predictions. For all regressions, grid cells were used as the unit of analysis. To test the niche divergence hypothesis, we first regressed mean absolute SSD against the species richness of each grid cell. Next, we fit a model that included an interaction between species richness and elevation range within cells to determine whether the slope of the mean absolute SSD–species richness relationship was greater in areas with small elevational ranges. We repeated the above using SVL spacing, rather than species richness. To test the reproductive selection hypotheses, we fit regression models relating mean SSD, mean clutch size, and mean male and female size to each climate variable. We also tested if mean SSD was related to mean

196 clutch mass across grid cells. As mean annual temperature and mean annual precipitation were the
197 only variables that showed a relationship with any of our dependent variables (see Results), we also
198 fit multiple regressions with these two variables and their interaction as predictors. Mean annual
199 precipitation and SVL spacing were log-transformed to help meet regression assumptions. In all
200 regressions, we weighted data points by the inverse standard error of the response variable in the
201 relevant grid cell. This accounts for variability in mean SSD (or mean SVL or mean log clutch mass)
202 within a cell by assigning lower weights to grid cells where means were less certain. Regressions
203 were limited to grid cells with at least two species with SSD data to allow standard errors to be
204 calculated, leaving 925 (100km x 100km), 3516 (50km x 50km), and 245 (200km x 200km) grid cells
205 for SSD and SVL analyses and 874, 3353, and 236 grid cells for clutch mass analyses.
206
207 **Randomisation Tests**
208 We tested the significance of regression relationships using an evolutionarily-informed randomisation
209 (Warren et al. 2014), that accounts for spatial and phylogenetic non-independence. Analyses that
210 apply trait data across species' ranges are sensitive to spurious patterns and inflated Type I error rates,
211 even when spatial regression methods are used, because of the spatial cohesiveness of species' ranges
212 (Hawkins et al. 2017). Type I errors can also arise because of difference in species richness among
213 grid cells, as areas with greater species richness, even when community assembly is random, tend to
214 approach the modal value (e.g. if most species are small, areas with high richness are constrained to
215 have low mean body sizes, but low richness grid cells can contain large or small average body sizes
216 (Meiri and Thomas 2007). Null models that maintain range size and cohesiveness and species
217 richness by randomly shuffling trait values can alleviate these problems by identifying relationships
218 that are stronger (or not) than expected due to sampling effects alone. However, they do not consider
219 phylogenetic non-independence. This can be important because species that occur closely in space are
220 also likely to be closely related and thus may share similar trait values (Warren et al. 2014). To
221 account for this problem, we simulated Brownian motion of SSD along the lizard phylogeny and used
222 the modelled SSD values at the tree's tips to recompute geographical patterns in mean SSD, thereby
223 generating a null distribution against which to compare the observed relationships (Warren et al.

2014). This approach maintains the spatial autocorrelation of SSD data that arises from range cohesion and ranges that span multiple cells, while accounting for sampling effects due to species richness differences among cells and for phylogenetic non-independence. We repeated this process for male SVL, female SVL, and log clutch mass for regressions where these were the dependent variables

To carry out our randomisation tests, we simulated Brownian motion of SSD (or SVL or log clutch mass) along Tonini et al.'s (2016) consensus phylogenetic tree. Nineteen species in our dataset were absent from the tree. We grafted these species on to the phylogeny as a sister to their closest relative in the tree at a random location along their terminal branch, or randomly within their shallowest clade affiliation, based on descriptions in the literature (Grummer and Bryson 2014, Köhler et al. 2014, 2015, 2016, Montanucci 2015, Campbell and Frost 2016, Solano-Zavaleta et al. 2016, Lara-Tufiño et al. 2016, Díaz-Cárdenas et al. 2017, Gottscho et al. 2017, Poe and Ryan 2017). A full list of placements is given in Supplementary material Appendix 1 Table A1. We used the fitContinuous function in Geiger v2.0.6 (Harmon et al. 2008) to estimate the mean SSD (or SVL or log clutch mass) at the phylogeny's root and the rate parameter (σ^2; Supplementary material Appendix 1 Table A2). We next used the fastBM function in phytools v0.6-44 (Revell 2012) to simulate Brownian motion using these parameters, assigned the simulated values to our species and recomputed the response variable across our cells. We next refit the regression to obtain t-values for the slope. We repeated this 1000 times and computed a two-tailed P-value for the observed relationship. We simulated log clutch mass, rather than clutch mass because simulating clutch mass produced many negative values which could then not be log-transformed (which itself suggests that the observed distribution of clutch mass is not simply a result of Brownian motion evolution).

RESULTS

SSD varied greatly across lizard species (Supplementary material Appendix 1 Fig. A2), from -0.76 (male-biased) in *Ctenosaura clarki* (male SVL: 250mm, female SVL: 142mm) to 0.52 (female-biased) in *Phrynosoma hernandesi* (male SVL: 82mm, female SVL: 125mm). SSD was female-biased

252 in 178 species and male-biased in 251 species. The sexes were of similar size (within 1%) in 34
253 species.
254
255 We found a clear geographical gradient in mean SSD from female-biased SSD in high latitude, colder
256 areas and male-biased SSD in warm, low latitude regions (Fig. 1). However, there were exceptions.
257 For example, mean SSD was male-biased at the high-latitude limit of lizards' ranges in one part of the
258 central USA. Qualitatively, mean SSD flipped from male-biased to female-biased around 31° latitude,
259 and mean annual temperature of approximately 15°C. As for previous work on lizard body size in
260 North America that did not consider sex, we did not find a clear latitudinal gradients in mean male or
261 female SVL (Olalla-Tarraga et al. 2006); geographical patterns of body size for males and females
262 were qualitatively similar (Fig. 2).
263
264 Mean SSD was negatively related to mean annual temperature, based on our randomization test
265 (P=0.03; Fig 3; Supplementary material Appendix 1 Table A3). Mean annual temperature explained
266 51% of the variance in mean SSD across North America (though this includes potential effects of
267 space and phylogeny). Mean SSD was not significantly related to any of the other climate variables
268 we tested (Fig 3; Supplementary material Appendix 1 Table A3), nor was it related log-transformed
269 clutch mass (Fig. 3; Supplementary material Appendix 1 Table A3). We found no interaction effect
270 on mean SSD between mean annual temperature and mean annual precipitation (Supplementary
271 material Appendix 1 Table A4). These results were consistent at all grain sizes (Supplementary
272 material Appendix 1 Tables A3-A4). The completeness of our SSD data (proportion of species in a
273 grid cell with SSD data) varied between 0.66 and 1.0 (median=0.95), with the most complete data in
274 north-eastern North America (Supplementary material Appendix 1 Fig. A3). However, this variation
275 in sampling is not responsible for the relationship between mean SSD and mean annual temperature,
276 as the relationship remains even after accounting for the proportion of species with SSD data in grid
277 cell, using partial regression (Supplementary material Appendix 1 Fig. A3).
278

279 Female mean SVL was not significantly related to any of the climate variables after accounting for
280 space and phylogeny via randomisation, regardless of grain size (Fig. 4; Supplementary material
281 Appendix 1 Table A3). In contrast, male mean SVL was greater in warmer areas, with mean annual
282 temperature explaining 59% of the variance in male mean SVL (P=0.01; Fig. 4; Supplementary
283 material Appendix 1 Table A3). This relationship held in 50km x 50km and 200km x 200km grid
284 cells (Supplementary material Appendix 1 Table A3). Log clutch mass was related to mean annual
285 precipitation, not temperature, with heavier clutches in drier, areas (P=0.04; Supplementary material
286 Appendix 1 Table A3 and Fig. A4). This relationship was similar across grain sizes (Supplementary
287 material Appendix 1 Tables A3). We found no relationship between mean log clutch mass and mean
288 annual temperature in a multiple regression, either as a main effect or interaction (Supplementary
289 material Appendix 1 Tables A4).
290
291 We found no relationship between mean absolute SSD, i.e. the magnitude of SSD regardless of
292 direction, and species richness at any spatial resolution (P>0.6, and R^2<0.08 for all; Fig. 5). We also
293 found no interaction effect of species richness and elevation range on mean absolute SSD (P>0.6 for
294 all grain sizes, Supplementary material Appendix 1 Table A5). Mean absolute SSD was unrelated to
295 the SVL spacing of species in all grid cell sizes (P>0.9 for all; see Fig. 5 for results at 100km x
296 100km). We found no interaction effect between SVL spacing and elevation range at any resolution
297 (P>0.35 for all; Supplementary material Appendix 1 Table A6).
298
299 **DISCUSSION**
300 We found a continental-scale gradient in lizard sexual size dimorphism that included a switch from
301 female-biased SSD in cold environments to male-biased SSD in warm ones. This gradient was related
302 to mean annual temperature, which also reflects the potential length of breeding season in reptiles and
303 other taxa (Meiri et al. 2013, Machado et al. 2016). This biogeographical pattern cannot be explained
304 as a by-product of Brownian motion evolution, the cohesive structure of species' ranges, or sampling
305 effects due to species richness differences. It thus likely reflects differences in the evolutionary rate

306 and/or trajectory of male and female size differences along the continental temperature gradient that
307 are consistent with differential selection on reproductive success of males and females.
308
309 The switch from male-biased SSD to female-biased SSD at mid-latitudes in North America is similar
310 to the global pattern in birds, which also have female-biased SSD, or low male-biased SSD, at high
311 latitudes (Friedman and Remeš 2016). However, the lizard and bird SSD gradients are not identical.
312 In particular, Friedman and Remeš (2016) found only a very weak global association between climate
313 (including mean annual temperature) and avian SSD,. The strength of this relationship varied by
314 biogeographic realm, but was weak, or non-existent, within the Nearctic and Neotropics. However,
315 Friedman and Remeš (2016) did not analyse these realms together, as we did; the greater female-bias
316 in bird SSD in the Nearctic relative to the Neotropics is roughly collinear with the continental
317 temperature gradient. Of course, other differences between lizards and birds could be responsible for
318 differences in how SSD relates to temperature. Thermoregulatory strategy—ectothermy versus
319 endothermy—is a tempting hypothesis, but differences could also arise from flight capacity, dispersal
320 ability, migratory behaviour, diet variation, microhabitat use, mating system and so on.
321
322 The lizard SSD gradient we observed is consistent with the reproductive selection hypothesis,
323 suggesting continental scale variation in climate does exert pressure on traits related to reproduction
324 (Macías-Ordóñez et al. 2013, Machado et al. 2016). However, our findings are not entirely clear on
325 the relative roles of female fecundity selection and male sexual selection. Fecundity selection imposed
326 by a short reproductive season in seasonal environments should favour larger reproductive output
327 within a limited time frame (Shine 1988, Pincheira-Donoso and Tregenza 2011). As larger females
328 can produce larger clutches and/or offspring (Meiri et al. 2012), shorter breeding seasons should thus
329 select for larger females, leading to female-biased SSD in cold, seasonal environments, as observed.
330 However, other lines of evidence suggest the fecundity selection is not the complete story. First,
331 female body size varied little in response to the continental temperature gradient. Second, clutch mass
332 varied with mean annual precipitation, but it was unrelated to temperature, the latter being a stronger
333 predictor of SSD. As such, clutch mass and SSD were not correlated, as we would expect if selection

for greater clutch mass was producing female-biased SSD. SSD and clutch mass could be decoupled for several reasons. In particular, females can achieve larger clutches by increasing the size of their abdominal cavity with little increase in their snout-vent length (Scharf and Meiri 2013), which then wouldn't affect SVL-based measures of SSD. An increase in species exhibiting viviparity in cold environments (Meiri et al. 2013, Pincheira-Donoso et al. 2013), which also leads to less frequent clutches, could have also contributed to the SSD gradient. The lack of relationship between SSD and clutch mass suggests that female-biased SSD can arise for reasons other than, or in addition to, fecundity selection (Pincheira-Donoso and Hunt 2017).

The SSD gradient predominantly reflects variation in male size rather than in female size. SSD and male SVL both varied with mean annual temperature, while female SVL did not, though the relationship between male SVL and temperature was much weaker than that of SSD. Still, while our findings must be interpreted cautiously, males tended to be smaller in cooler, more seasonal areas, contradicting Olalla-Tarraga et al.'s (2006) analysis of body size variation (ignoring sex) in North American lizards. However, our analysis included Mexico and Central America, where male lizards, on average, tend to be large, whereas Olalla-Tarraga's et al.'s (2006) only included the USA and Canada. The patterns we observe in the USA are similar to theirs. While female size closely tracked the male pattern, there was insufficient variation in female SVL through space to recover a significant relationship with temperature. Greater variation in males than females is common in studies of sexual dimorphism and is consistent with, if not entirely indicative of, Rensch's rule, which states that when males are larger than females, SSD increases with body size and when females are larger, SSD decreases with body size (Abouheif and Fairbairn 1997, Blanckenhorn et al. 2006).

The gradient in SSD and male size is consistent with stronger sexual selection, via male-male competition, in warmer environments that lack a prolonged cold season. We found no relationship with precipitation seasonality, suggesting differences between dry and wet seasons are less important than temperature variation for sexual size dimorphism; this could be because lizards, in general (though there are exceptions), are able to effectively exploit dry environments (Roll et al. 2017).

362 Sexual selection may act directly on male size, if larger males are able to control higher quality
363 territories or access to females. It could also act indirectly, via traits like head size; larger heads
364 increase bite force and combat success in lizards (Herrel et al. 1999, Scharf and Meiri 2013, Lopez-
365 Darias et al. 2014). Sexual selection on males could be higher in warm, aseasonal environments
366 because the abundance and continual access to resources lessens the relative strength of viability
367 selection or because when resources and reproductive opportunities are available year round, there
368 may be greater total benefit for males that can control high-quality territories and access to mates
369 (Machado et al. (2016). Female lizards tend to have more clutches, spread through the year, in warm,
370 aseasonal, environments (Mesquita et al. 2016), which fits with this hypothesis and suggests that
371 gradients in male sexual selection are not decoupled from female fecundity selection.
372
373 Overall, while the patterns of SSD and male size we uncovered are consistent with the reproductive
374 selection hypothesis, especially a gradient in sexual selection, the evidence is indirect and other
375 processes could produce the same pattern. Inverse Bergmann's clines (smaller body size in cold
376 environments), like that observed here for males, are far from ubiquitous in lizards, but nor are they
377 rare (Ashton and Feldman 2003, Cruz et al. 2005, Olalla-Tarraga et al. 2006, Pincheira-Donoso and
378 Meiri 2013, Muñoz et al. 2014). Hypotheses have been proposed to explain these clines based on
379 thermoregulatory requirements, via heating and cooling rates, and resource availability (Ashton and
380 Feldman 2003, Sears and Angilletta 2004). Gradients in SSD along temperature gradients could arise
381 if these pressures exert stronger selection on males, or males exhibit greater responses to selection.
382 For example, in some species, gravid females thermoregulate more precisely (Beuchat 1986) and may
383 maintain different body temperatures than males (Shine 1980, Beuchat 1986, Schwarzkopf and Shine
384 1991), which could alter body size gradients as females would operate under different temperatures
385 than males. Another hypothesis, which we propose, is that fecundity selection for larger female size
386 and reproductive output could oppose viability selection for smaller size in cold and seasonal
387 environments, leading to a flatter gradient in female size and an increase in female-biased SSD as
388 males become smaller in cold places. Data on proxies of sexual selection across temperature
389 gradients, such as territoriality, head size, mating system, or—best of all— direct measures of sexual

390 and fecundity selection in the field, are needed to test hypotheses for the biogeographical pattern we
391 have identified here.
392
393 The continental mean SSD gradient in lizards was not linked to species richness, at least at the coarse
394 grain size examined here. The niche divergence hypothesis proposes that selection favours size
395 divergence between males and females to limit intraspecific competition for similar resources
396 (Schoener 1977, Slatkin 1984, Shine 1989, Pincheira-Donoso et al. 2009, Meiri et al. 2014). Past
397 findings for this hypothesis are mixed across taxa, including lizards: Schoener (1977) found evidence
398 consistent with this pattern for *Anolis* lizards on small Caribbean islands, but a more recent
399 geographically and taxonomically comprehensive analysis did not find lower SSD on species-rich
400 islands (Meiri et al. 2014). Our results are consistent with Meiri et al.'s (2014) findings. Instead of a
401 negative correlation between SSD and species richness, we found a funnel-shaped relationship
402 between absolute SSD and species richness, which is consistent with the expected sampling effects of
403 species richness on SSD. When richness is low, mean SSD can be either high or low, but as richness
404 increases, SSD is increasingly constrained to be closer to the mean. Thus, we found no evidence of a
405 negative relationship between SSD and richness. Pincheira-Donoso et al. (2018) found a relationship
406 between SSD and richness in local assemblages of *Liolaemus* lizards. They suggested that the mixed
407 evidence for the niche divergence hypothesis reflects differences in spatial and ecological scales,
408 where effects of competition on inter-sexual niche divergence will only appear at local scales (also
409 see De Lisle and Rowe 2015). It is thus possible that the species richness of large grid cells, as used
410 here, does not accurately reflect the number of competitors that a species interacts with. This may
411 especially be true in mountainous areas with large environmental gradients and high species turnover.
412 However, our results suggest that the SSD–richness relationship it not stronger in flatter areas where
413 we would expect grid cell richness to better reflect local richness. This suggests either that intersexual
414 niche divergence is not constrained by interspecific competitors, that its effects are not strong enough
415 to leave a signature at macroecological scales, that range maps are too coarse to capture richness
416 patterns accurately, or that species richness is a poor proxy for the ecological opportunities available
417 for intersexual niche divergence (Meiri et al. 2014). Related to this final point, we found no

relationship between SVL spacing, i.e. species packing, and mean absolute SSD. If interspecific competition was constraining SSD, as posited by the niche divergence hypotheses, then SSD should have been lower when species in a grid cell are more similarly sized, but it was not. Our findings suggest that, while competitive processes may be important at local scales, or within guilds, selection on reproductive success is a more likely explanation for broader, continental scale SSD gradients than competition-driven niche divergence.

Classically, studies of macroecological variation in body size across broad geographical extents have ignored sex. Our finding that the direction of SSD switches from larger males to larger females along a temperature gradient stresses the importance of considering sex in macroecological investigations of body size and other traits as the sexes respond differently to the selection pressures imposed along climate gradients. The switch from male-biased SSD to female-biased SSD at mid-latitudes is more than reminiscent of the pattern found in birds worldwide (Friedman and Remeš 2016), hinting at a general pattern across major taxonomic boundaries. The biogeographical reversal from female-biased SSD in the north to male-biased SSD in the south opens up new avenues to understand how environment affects the origin and maintenance of sexual size dimorphism, the evolutionary processes that underlie it, and the geographical distribution of body size.

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Redacted to maintain anonymity of authors.

REFERENCES

Abouheif, E. and Fairbairn, D. 1997. A comparative analysis of allometry for sexual size dimorphism: assessing Rensch's rule. - Am. Nat. 149: 540–562.

Algar, A. C. and López-Darias, M. 2016. Sex-specific responses of phenotypic diversity to environmental variation. - Ecography (Cop.). 39: 715–725.

Ashton, K. G. and Feldman, C. R. 2003. Bergmann's rule in nonavian reptiles: turtles follow it, lizards and snakes reverse it. - Evolution 57: 1151–1163.

Berry, J. F. and Shine, R. 1980. Sexual size dimorphism and sexual selection in turtles (Order

446 Testudines). - Oecologia 44: 185–191.
447 Beuchat, C. A. 1986. Reproductive influences on the thermoregulatory behavior of a live-bearing
448 lizard. - Copeia 1986: 971–979.
449 Blanckenhorn, W. U. et al. 2006. When Rensch meets Bergmann: does sexual size dimorphism
450 change systematically with latitude? - Evolution 60: 2004–2011.
451 Butler, M. A. et al. 2000. The relationship between sexual size dimorphism and habitat use in Greater
452 Antillean Anolis lizards. - Evolution 54: 259–272.
453 Campbell, J. A. and Frost, D. R. 2016. A new species of *Abronia* (Squamata: Anguidae) from the
454 Sierra Madre del Sur of Oaxaca, Mexico. - J. Herpetol. 50: 149–156.
455 Cardillo, M. 2002. The life-history basis of latitudinal diversity gradients: how do species traits vary
456 from the poles to the equator? - J. Anim. Ecol. 71: 79–87.
457 Cox, R. M. et al. 2003. A comparative test of adaptive hypotheses for sexual size dimorphism in
458 lizards. - Evolution 57: 1653–1669.
459 Cox, R. M. et al. 2007. The evolution of sexual size dimorphism in reptiles. - In: Fairbairn, D. J. et al.
460 (eds), Sex, size and gender roles: evolutionary studies of sexual size dimorphism. Oxford
461 University Press, pp. 38–49.
462 Cruz, F. B. et al. 2005. The importance of phylogenetic scale in tests of Bergmann's and Rapoport's
463 rules: lessons from a clade of South American lizards. - J. Evol. Biol. 18: 1559–1574.
464 Currie, D. J. 1991. Energy and large-scale patterns of animal-species and plant-species richness. -
465 Am. Nat. 137: 27–49.
466 Dayan, T. and Simberloff, D. 2005. Ecological and community-wide character displacement: the next
467 generation. - Ecol. Lett. 8: 875–894.
468 De Lisle, S. P. and Rowe, L. 2015. Independent evolution of the sexes promotes amphibian
469 diversification. - Proc. R. Soc. B Biol. Sci. 282: 20142213.
470 Díaz-Cárdenas, B. et al. 2017. Species delimitation of the blue-spotted spiny lizard within a
471 multilocus, multispecies coalescent framework, results in the recognition of a new *Sceloporus*
472 species. - Mol. Phylogenet. Evol. 111: 185–195.
473 Fairbairn, D. J. 2007. Introduction: the enigma of sexual size dimorphism. - In: Fairbairn, D. J. et al.

(eds), Sex, Size and Gender Roles: Evolutionary Studies of Sexual Size Dimorphism. Oxford University Press, pp. 1–10.

Fitch, H. S. 1976. Sexual size differences in the mainland anoles. - Occas. Pap. Museum Nat. Hist. Univirsity Kansas 50: 1–21.

Fitch, H. S. 1981. Sexual size differences in reptiles. - Kansas Museum of Natural History.

Fitch, H. S. and Hillis, D. M. 1984. The *Anolis* dewlap: interspecific variability and morphological associations with habitat. - Copeia 1984: 315–323.

Friedman, N. R. and Remeš, V. 2016. Global geographic patterns of sexual size dimorphism in birds: Support for a latitudinal trend? - Ecography (Cop.). 39: 17–25.

Gottscho, A. D. et al. 2017. Lineage diversification of fringe-toed lizards (Phrynosomatidae: *Uma notata* complex) in the Colorado Desert: delimiting species in the presence of gene flow. - Mol. Phylogenet. Evol. 106: 103–117.

Grummer, J. A. and Bryson, R. W. 2014. A new species of bunchgrass lizard (Squamata: Phrynosomatidae) from the southern sky islands of the Sierra Madre Occidental, Mexico. - Zootaxa 3790: 439–450.

Harmon, L. J. et al. 2008. geiger: analysis of evolutionary diversification. - Bioinformatics 24: 129–131.

Hawkins, B. A. et al. 2017. Structural bias in aggregated species-level variables driven by repeated species co-occurrences: a pervasive problem in community and assemblage data. - J. Biogeogr. 44: 1199–1211.

Hedrick, A. V. and Temeles, E. J. 1989. The evolution of sexual dimorphism in animals: hypotheses and tests. - Trends Ecol. Evol. 4: 136–138.

Herrel, A. et al. 1999. Sexual dimorphism of head size in *Gallotia galloti*: testing the niche divergence hypothesis by functional analyses. - Funct. Ecol. 13: 289–297.

Hijmans, R. J. et al. 2005. Very high resolution interpolated climate surfaces for global land areas. - Int. J. Climatol. 25: 1965–1978.

Köhler, G. et al. 2014. Two new species of the *Norops pachypus* complex (Squamata , Dactyloidae) from Costa Rica. - Mesoamerican Herpetol. 1: 254–280.

502 Köhler, J. J. et al. 2015. *Anolis marsupialis* Taylor 1956, a valid species from southern Pacific Costa
503 Rica (Reptilia, Squamata, Dactyloidae). - Zootaxa 3915: 111–122.
504 Köhler, G. et al. 2016. Taxonomic revision of the *Norops tropidonotus* complex (Squamata,
505 Dactyloidae), with the resurrection of *N. spilorhipis* (Alvarez del Toro and Smith, 1956) and the
506 description of two new species. - Mesoamerican Herpetol. 3: 8–41.
507 Lara-Tufiño, J. D. et al. 2016. Resurrection of *Anolis ustus* Cope, 1864 from synonymy with *Anolis*
508 *sericeus* Hallowell, 1856 (Squamata, Dactyloidae). - Zookeys 619: 147–162.
509 Lopez-Darias, M. et al. 2014. Sex-specific differences in ecomorphological relationships in lizards of
510 the genus *Gallotia*. - Funct. Ecol. 29: 506–514.
511 Losos, J. B. 2009. Lizards in an Evolutionary Tree: Ecology and Adaptive Radiation of Anoles. -
512 University of California Press.
513 Lovich, J. E. and Gibbons, J. W. 1992. A review of techniques for quantifying sexual size
514 dimorphism. - Growth, Dev. Aging 56: 269–81.
515 Machado, G. et al. 2016. Macroecology of sexual selection: a predictive conceptual framework for
516 large-scale variation in reproductive traits. - Am. Nat. 188: S8–S27.
517 Macías-Ordóñez, R. et al. 2013. Macroecology of sexual selection: large-scale influence of climate on
518 sexually selected traits. - In: Sexual Selection: Perspectives and Models from the Neotropics.
519 Academic Press, pp. 1–32.
520 Meiri, S. 2008. Evolution and ecology of lizard body sizes. - Glob. Ecol. Biogeogr. 17: 724–734.
521 Meiri, S. 2018. Traits of lizards of the world: Variation around a successful evolutionary design. -
522 Glob. Ecol. Biogeogr. in press.
523 Meiri, S. and Thomas, G. H. 2007. The geography of body size – challenges of the interspecific
524 approach. - Glob. Ecol. Biogeogr. 16: 689–693.
525 Meiri, S. et al. 2012. The ecology of lizard reproductive output. - Glob. Ecol. Biogeogr. 21: 592–602.
526 Meiri, S. et al. 2013. Are lizards feeling the heat? A tale of ecology and evolution under two
527 temperatures. - Glob. Ecol. Biogeogr. 22: 834–845.
528 Meiri, S. et al. 2014. The number of competitor species is unlinked to sexual dimorphism. - J. Anim.
529 Ecol. 83: 1302–1312.

530 Mena, J. L. and Vázquez-Domínguez, E. 2005. Species turnover on elevational gradients in small
531 rodents. - Glob. Ecol. Biogeogr. 14: 539–547.
532 Mesquita, D. O. et al. 2016. Life-history patterns of lizards of the world. - Am. Nat. 187: 689–705.
533 Montanucci, R. R. 2015. A taxonomic revision of the *Phrynosoma douglasii* species complex
534 (Squamata: Phrynosomatidae). - Zootaxa 4015: 1–177.
535 Muñoz, M. M. et al. 2014. Untangling intra- and interspecific effects on body size clines reveals
536 divergent processes structuring convergent patterns in *Anolis lizards*. - Am. Nat. 184: 636–646.
537 Olalla-Tarraga, M. A. et al. 2006. Broad-scale patterns of body size in squamate reptiles of Europe
538 and North America. - J. Biogeogr. 33: 781–793.
539 Pianka, E. R. and Vitt, L. J. 2003. Lizards: Windows to the Evolution of Diversity. - University of
540 California Press.
541 Pietsch, T. W. 2005. Dimorphism, parasitism, and sex revisited: modes of reproduction among deep-
542 sea ceratioid anglerfishes (Teleostei: Lophiiformes). - Ichthyol. Res. 52: 207–236.
543 Pincheira-Donoso, D. and Tregenza, T. 2011. Fecundity selection and the evolution of reproductive
544 output and sex-specific body size in the Liolaemus lizard adaptive radiation. - Evol. Biol. 38:
545 197–207.
546 Pincheira-Donoso, D. and Meiri, S. 2013. An intercontinental analysis of climate-driven body size
547 clines in reptiles: no support for patterns, no signals of processes. - Evol. Biol. 40: 562–578.
548 Pincheira-Donoso, D. and Hunt, J. 2017. Fecundity selection theory: concepts and evidence. - Biol.
549 Rev. 92: 341–356.
550 Pincheira-Donoso, D. et al. 2009. A phylogenetic analysis of sex-specific evolution of ecological
551 morphology in Liolaemus lizards. - Ecol. Res. 24: 1223–1231.
552 Pincheira-Donoso, D. et al. 2013. The evolution of viviparity opens opportunities for lizard radiation
553 but drives it into a climatic cul-de-sac. - Glob. Ecol. Biogeogr. 22: 857–867.
554 Pincheira-Donoso, D. et al. 2018. Sexes and species as rival units of niche saturation during
555 community assembly. - Glob. Ecol. Biogeogr. 27: 593–603.
556 Poe, S. and Ryan, M. J. 2017. Description of two new species similar to *Anolis insignis* (Squamata:
557 Iguanidae) and resurrection of *Anolis (Diaphoranolis) brooksi*. - Amphib. Reptile Conserv. ll: 1–

16.

Revell, L. J. 2012. phytools: an R package for phylogenetic comparative biology (and other things). - Methods Ecol. Evol. 3: 217–223.

Roll, U. et al. 2017. The global distribution of tetrapods reveals a need for targeted reptile conservation. - Nat. Ecol. Evol. 1: 1677–1682.

Scharf, I. and Meiri, S. 2013. Sexual dimorphism of heads and abdomens: different approaches to 'being large' in female and male lizards. - Biol. J. Linn. Soc. 110: 665–673.

Schoener, T. W. 1977. Competition and the niche. - In: Gans, C. and Tinkle, D. (eds), Biology of the Reptilia, Volume 7: Ecology and Behaviour A. Academic Press, pp. 35–136.

Schwarz, R. and Meiri, S. 2017. The fast-slow life-history continuum in insular lizards: a comparison between species with invariant and variable clutch sizes. - J. Biogeogr. 44: 2808–2815.

Schwarzkopf, L. and Shine, R. 1991. Thermal biology of reproduction in viviparous skinks, *Eulamprus tympanum*: why do gravid females bask more? - Oecologia 88: 562–569.

Sears, M. W. and Angilletta, M. J. 2004. Body size clines in *Sceloporus* lizards: proximate mechanisms and demographic constraints. - Integr. Comp. Biol. 44: 433–42.

Shine, R. 1978. Sexual size dimorphism and male combat in snakes. - Oecologia 33: 269–277.

Shine, R. 1980. "Costs" of reproduction in reptiles. - Oecologia 46: 92–100.

Shine, R. 1988. The evolution of large body size in females: a critique of Darwin's "fecundity advantage" model. - Am. Nat. 131: 124–131.

Shine, R. 1989. Ecological causes for the evolution of sexual dimorphism: a review of the evidence. - Q. Rev. Biol. 64: 419–461.

Shine, R. 1994. Sexual size dimorphism in snakes revisited. - Copeia 1994: 326–346.

Slatkin, M. 1984. Ecological causes of sexual dimorphism. - Evolution 38: 622–630.

Solano-Zavaleta, I. et al. 2016. A New species of Mesaspis (Squamata: Anguidae) from the High Cuchumatanes of Guatemala. - J. Herpetol. 50: 327–336.

Stamps, J. A. 1983. Sexual selection, sexual dimorphism and territoriality. - In: Pianka, E.R., Schoener, T. W. (ed), Lizard Ecology: Studies of a Model Organism. Harvard University Press, pp. 169–204.

586 Stillwell, R. C. et al. 2007. Geographic variation in body size and sexual size dimorphism of a seed-
587 feeding beetle. - Am. Nat. 170: 358–369.
588 Storz, J. F. et al. 2001. Clinal variation in body size and sexual dimorphism in an Indian fruit bat,
589 *Cynopterus sphinx* (Chiroptera: Pteropodidae). - Biol. J. Linn. Soc. 72: 17–31.
590 Title, P. O. and Bemmels, J. B. 2018. ENVIREM: an expanded set of bioclimatic and topographic
591 variables increases flexibility and improves performance of ecological niche modeling. -
592 Ecography (Cop.). 41: 291–307.
593 Tonini, J. F. R. et al. 2016. Fully-sampled phylogenies of squamates reveal evolutionary patterns in
594 threat status. - Biol. Conserv. 204: 23–31.
595 Warren, D. L. et al. 2014. Mistaking geography for biology: Inferring processes from species
596 distributions. - Trends Ecol. Evol. 29: 572–580.
597

598 **SUPPLEMENTARY INFORMATION**

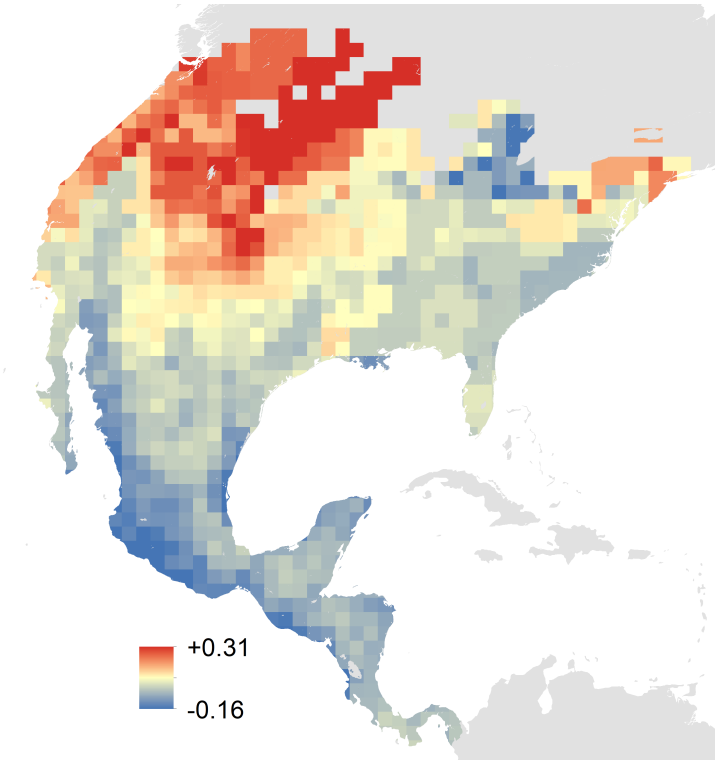
599 Supplementary material (Appendix EXXXXX at <www.oikosoffice.lu.se/appendix>). Appendix 1.
600

601 **DATA ACCESSIBILITY**

602 All data used in this manuscript are available via Meiri (2018), Roll et al. (2017), and Hijmans et al.
603 (2005). A list of species is given in Supplementary material Appendix 1 Table A7.
604

605 **Figures**

606



607

608 Figure 1. Geographical patterns in mean sexual size dimorphism of lizards in 100km x 100km cells
609 across Central and North America (Mollweide projection). Sexual size dimorphism is positive (red)
610 when females are larger than males and negative (blue) when males are larger than females.

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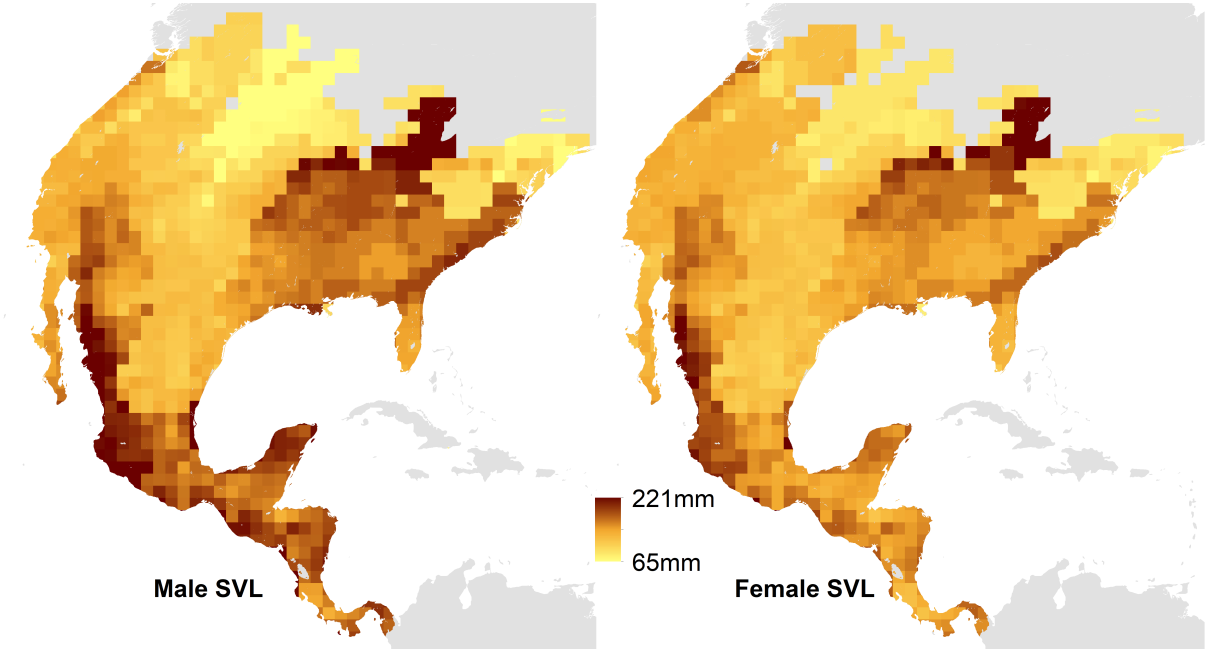

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615 Figure 2. Geographical patterns of mean body size (snout-vent length; SVL in mm) of male (left) and
616 female (right) lizards in 100km x 100km grid cells across Central and North America (Mollweide
617 projection). Colour scales are identical in both panels.

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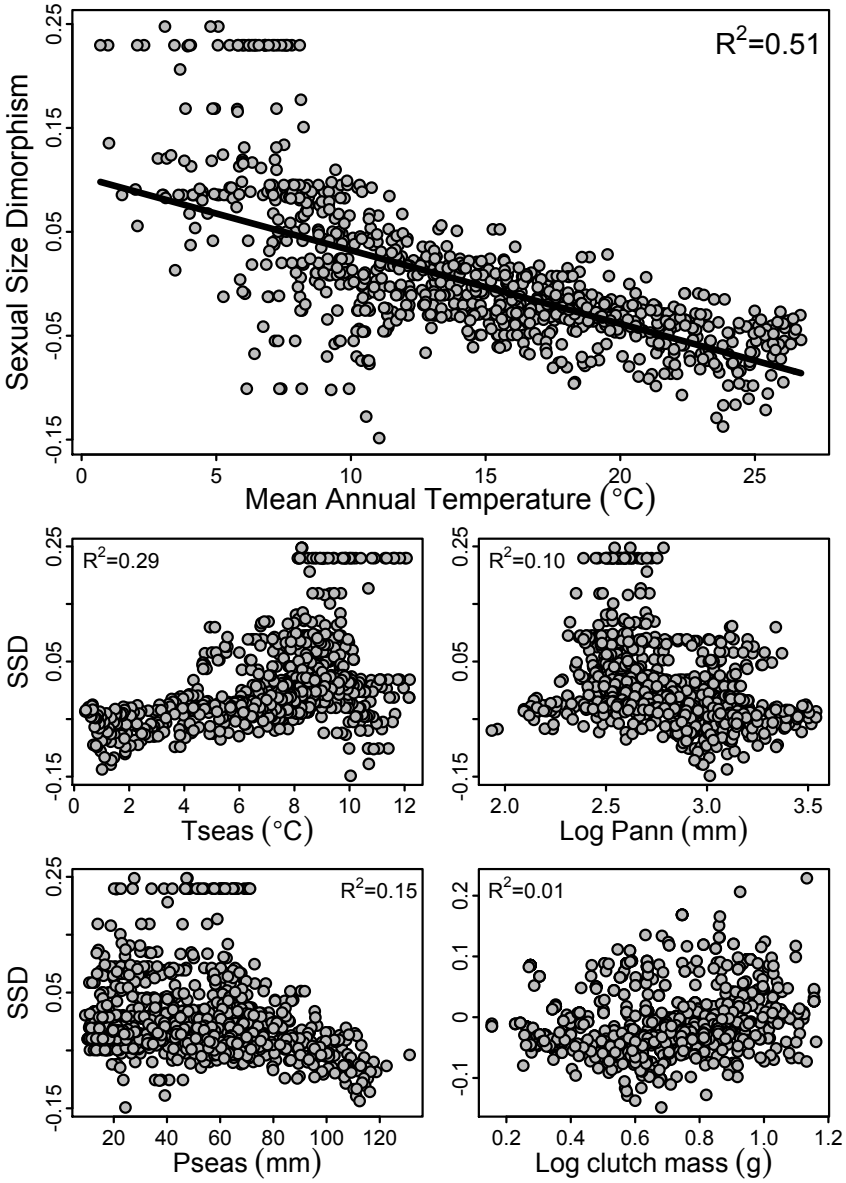

620

621 Figure 3. Relationships between sexual size dimorphism (SSD) and climate for lizards in 100km x
622 100km grid cells across North and Central America. Only the SSD–mean annual temperature
623 relationship was significant (P=0.03; black regression line) relative to the expectation under a
624 Brownian motion evolution of SSD. When SSD is positive, females are larger than males; when it is
625 negative, males are larger than females. Tseas is temperature seasonality, Pann is mean annual
626 precipitation, and Pseas is precipitation seasonality.

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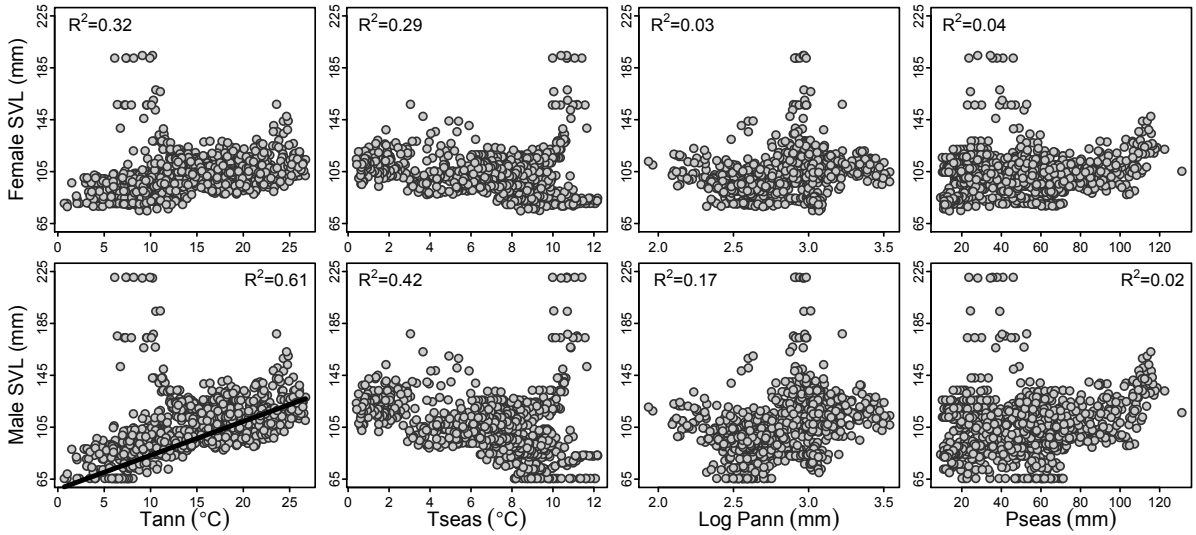

629

630 Figure 4. Relationships between sex-specific mean body size (snout–vent length; SVL) and climate
631 for lizards in 100km x 100km grid cells across North and Central America. The relationship between
632 male SVL and mean annual temperature (black line) had P=0.01 relative to the expectation under
633 Brownian motion evolution. Tann is mean annual temperature, Tseas is temperature seasonality, Pann
634 is mean annual precipitation and Pseas is precipitation seasonality.

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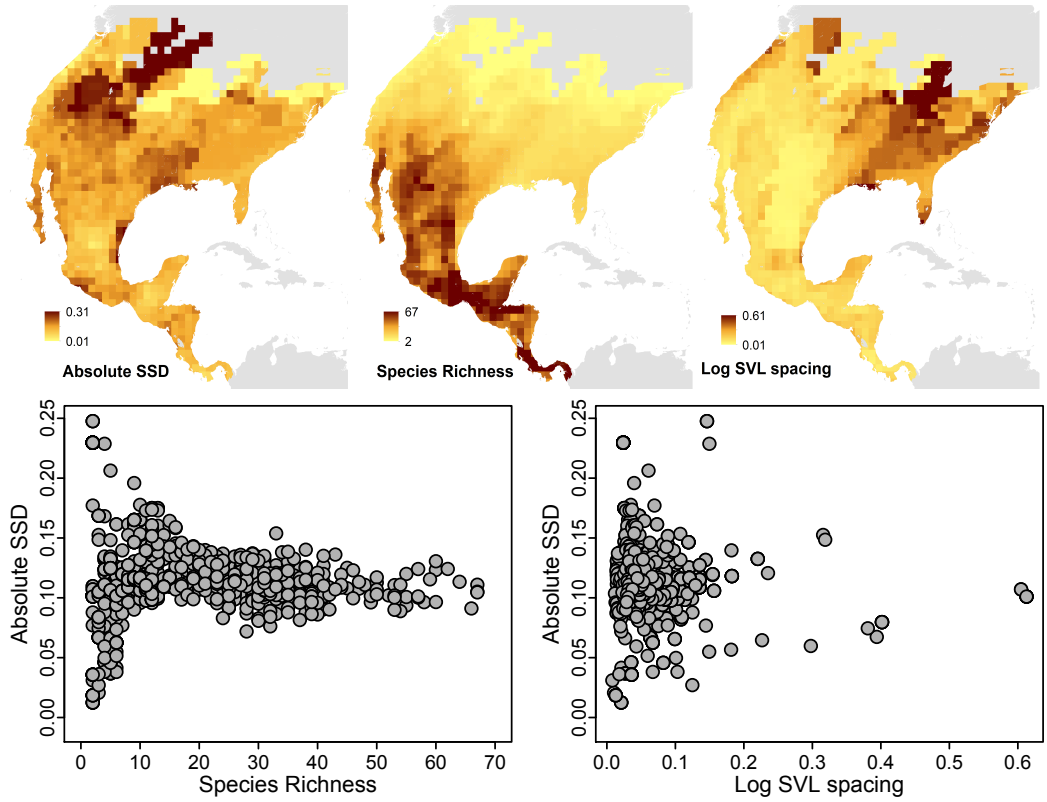

637

638 Figure 5. Geographical gradients in the magnitude of sexual size dimorphism, regardless of direction
639 (absolute SSD), species richness, and SVL (snout–vent length) spacing (mean body size ratio of
640 adjacently-sized species) of lizards in 100km x 100km grid cells across Central and North America
641 (Mollweide projection). Absolute SSD ignores the direction of sexual size dimorphism (whether
642 males or females are larger). SVL spacing is shown on a log scale. Absolute SSD was not
643 significantly related to species richness (P=0.79) or log SVL spacing (P=0.99).

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SUPPLEMENTARY MATERIAL

A biogeographic reversal in sexual size dimorphism along a continental temperature gradient

Appendix 1: Supplementary Tables and Figures

Table A1. Placement of species missing from phylogeny.

Species	Comment	Reference
Abronia cuetzpali	Most closely related to *oaxaca* and *mixteca*, most similar to *mixteca* according to Campbell et al. so add as sister to *mixteca*	Campbell, J.A., et al. 2016. A new species of *Abronia* (Squamata: Anguidae) from the Sierra Madre del Sur of Oaxaca, Mexico. Journal of Herpetology 50: 149-156.
Anolis alocomyos & Anolis leditzigorum	Both formerly part of *tropidolepis*, make a random clade with *tropidolepis*	Köhler, G., et al. 2014. Two new species of the *Norops pachypus* complex (Squamata, Dactyloidae) from Costa Rica. Mesoamerican Herpetology 1: 254–280.
Anolis brooksi & Anolis kathydayae	Part of a clade with *microtus* and *ginaelisae* so make a random clade with these & *brooksi* & *kathydayae*, based on Poe & Ryan.	Poe S, Ryan M.J. 2017. Description of two new species similar to *Anolis insignis* (Squamata: Iguanidae) and resurrection of *Anolis* (*Diaphoranolis*) *brooksi*. Amphibian & Reptile Conservation 11: 1–16.
Anolis marsupialis	Part of a clade with *aquaticus* and *woodi* so make a random clade with these	Köhler, J.J., et al. 2015. *Anolis marsupialis* Taylor 1956, a valid species from southern Pacific Costa Rica (Reptilia, Squamata, Dactyloidae). Zootaxa 3915111–122
Anolis mccraniei, Anolis spilorhipis, & Anolis wilsoni	Formerly part of *tropidonotus*, so split *tropidonotus* into a random clade	Köhler, G., et al. 2016. Taxonomic revision of the *Norops tropidonotus* complex (Squamata, Dactyloidae), with the resurrection of *N. spilorhipis* (Alvarez del Toro and Smith, 1956) and the description of two new species. Mesoamerican Herpetology 3: 8–41
Anolis ustus	Was synonym of *sericeus* but elevated to species so placed as sister to *sericeus*	Lara-Tufiño J.D., et al. 2016. Resurrection of *Anolis ustus* Cope, 1864 from synonymy with *Anolis sericeus* Hallowell, 1856 (Squamata, Dactyloidae). ZooKeys 619: 147–162.
Aspidoscelis costatus	synonym of *sackii* so add as sister to *sackii*	Reptile Database
Mesaspis cuchumatanus	most similar to *moreletii*, so add as sister thereof	Solano-Zavaleta, I., et al. 2016. A new species of *Mesaspis* (Squamata: Anguidae) from the high Cuchumatanes of Guatemala. Journal of Herpetology 50: 327-336
Phrynosoma bauri	Allied to *brevirostris*, add to clade with *hernandesi*, *brevirostris* and *diminutum*	Montanucci, R.R. 2015. A taxonomic revision of the *Phrynosoma douglasii* species complex (Squamata: Phrynosomatidae). Zootaxa 4015: 1–177
Phrynosoma brevirostris	Distinct from *hernandesi*, add to clade with *hernandesi*, *brevirostris* and *diminutum*	Montanucci, R.R. 2015. A taxonomic revision of the *Phrynosoma douglasii* species complex (Squamata: Phrynosomatidae). Zootaxa 4015: 1–177
Phrynosoma diminutum	allied to *brevirostris*, add to clade with *hernandesi*, *brevirostris* and *diminutum*	Montanucci, R.R. 2015. A taxonomic revision of the *Phrynosoma douglasii* species complex (Squamata: Phrynosomatidae). Zootaxa 4015: 1–177
Sceloporus brownorum	in *scalaris* group, but topology of Tonini et al. tree doesn't match Grummer et al. tree, so add next to *scalaris* rather than restructure the whole clade's topology	Grummer, J.A., et al. 2014. A new species of bunchgrass lizard (Squamata: Phrynosomatidae) from the southern sky islands of the Sierra Madre Occidental, Mexico. Zootaxa 3790: 439–450
Sceloporus gadsdeni	Split from *cyanostictus*, so add as a sister to this species	Díaz-Cárdenas, B., et al. 2017. Species delimitation of the blue-spotted spiny lizard within a multilocus, multispecies

		coalescent framework, results in the recognition of a new *Sceloporus* species. Molecular Phylogenetics and Evolution 111: 185-195
Sceloporus oberon	Paraphyletic with *minor* and *ornatus* which are sisters in tree so randomly add to this clade.	Díaz-Cárdenas, B., et al. 2017. Species delimitation of the blue-spotted spiny lizard within a multilocus, multispecies coalescent framework, results in the recognition of a new *Sceloporus* species. Molecular Phylogenetics and Evolution 111: 185-195
Uma cowlesi	According to Gottscho et al., *rufopunctata* is a hybrid between *cowlesi* and *notata*. *rufopunctata* is in the Tonini et al tree though, so add as sister to *rufopunctata*	Gottscho, A.D., et al. 2016. Lineage diversification of fringe-toed lizards (Phrynosomatidae: *Uma notata* complex) in the Colorado Desert: delimiting species in the presence of gene flow. Molecular Phylogenetics and Evolution 106: 103-117

Table A2. Parameters for Brownian motion simulations for randomisation tests.

Variable	Mean at root	σ^2
Sexual size dimorphism	-0.008	0.0017
Log Clutch mass	0.274	0.005
Male snout-vent length	111.8	92.4
Female snout-vent length	109.2	72.4

SUPPLEMENTARY MATERIAL

A biogeographic reversal in sexual size dimorphism along a continental temperature gradient

Table A3. Univariate regression results relating sexual size dimorphism, clutch mass, male and female size, and climate in grid cells of different grain sizes. Significance was determined based on the distribution of test statistics expected under Brownian motion evolution of the response variable. All P-values are two-tailed. Sexual size dimorphism is positive when females are larger. SVL is snout-vent length. Mean annual precipitation was log-transformed mean annual precipitation. P-values less than 0.05 are in bold.

	Response Variables											
	Sexual Size Dimorphism			Log Clutch Mass			Female SVL			Male SVL		
Predictor Variable	slope	P	r^2	slope	P	r^2	slope	P	r^2	slope	P	r^2
100km x 100km												
Mean annual temperature	**-0.007**	**0.03**	0.51	0.005	0.83	0.01	1.17	0.14	0.32	**2.61**	**0.01**	0.61
Temperature seasonality	1×10^{-4}	0.22	0.29	-1×10^{-5}	0.98	1×10^{-4}	-0.02	0.19	0.29	-0.05	0.08	0.42
Annual Precipitation	-0.06	0.58	0.10	**-0.59**	**0.04**	0.46	7.33	0.80	0.03	34.1	0.43	0.17
Precipitation seasonality	-8×10^{-4}	0.36	0.15	0.003	0.59	0.12	0.10	0.73	0.04	0.11	0.83	0.02
Log clutch mass	0.02	0.90	0.01	-	-	-	-	-	-	-	-	-
50km x 50km												
Mean annual temperature	**-0.007**	**0.03**	0.59	0.004	0.84	0.01	1.28	0.11	0.33	**2.6**	**0.01**	0.59
Temperature seasonality	1×10^{-4}	0.18	0.31	4×10^{-5}	0.96	0.01	-0.03	0.19	0.27	-0.05	0.05	0.42
Annual precipitation	-0.06	0.55	0.11	-0.55	0.05	0.42	9.9	0.74	0.05	29.5	0.46	0.16
Precipitation seasonality	-8×10^{-4}	0.38	0.16	0.003	0.60	0.12	0.11	0.71	0.05	0.16	0.74	0.03
Log clutch mass	-0.02	0.88	0.01	-	-	-	-	-	-	-	-	-
200km x 200km												
Mean annual temperature	-0.007	0.05	0.51	0.007	0.76	0.04	0.98	0.25	0.26	**2.5**	**0.03**	0.56
Temperature seasonality	1×10^{-4}	0.32	0.28	-1×10^{-5}	0.90	0.02	-0.02	0.33	0.25	-0.05	0.11	0.44
Annual precipitation	-0.05	0.64	0.07	**-0.6**	**0.04**	0.43	3.9	0.90	0.01	34.1	0.40	0.17
Precipitation seasonality	-8×10^{-4}	0.48	0.15	0.003	0.65	0.11	0.09	0.81	0.03	0.02	0.98	0.00
Log clutch mass	-0.03	0.87	0.02	-	-	-	-	-	-	-	-	-

SUPPLEMENTARY MATERIAL

A biogeographic reversal in sexual size dimorphism along a continental temperature gradient

Table A4. Multiple regression results relating sexual size dimorphism, clutch mass, and male and female size to mean annual temperature and annual precipitation in 100km x 100km cells. Significance was determined based on the distribution of test statistics expected under Brownian motion evolution of the response variable. All P-values are two-tailed. Sexual size dimorphism is positive when females are larger. SVL is snout-vent length. The interaction is between mean annual temperature and annual precipitation. P-values less than 0.05 are in bold.

	Response Variables											
	Sexual Size Dimorphism			Log Clutch Mass			Female SVL			Male SVL		
Predictor Variable	slope	P	R^2	slope	P	R^2	slope	P	r^2	slope	P	R^2
100km x 100km												
Model with interaction												
Mean annual temperature	-0.03	0.29		-0.009	0.95		0.005	0.99		6.2	0.53	
Annual precipitation	-0.18	0.64	0.58	-0.72	0.61	0.52	-4.3	0.96	0.32	36.4	0.69	0.66
Interaction	0.009	0.51		0.007	0.91		0.41	0.93		-1.4	0.75	
Model without interaction												
Mean annual temperature	**-0.006**	**0.05**	0.52	0.009	0.64	0.51	2.4	0.01	0.32	1.3	0.10	0.65
Annual precipitation	-0.013	0.92		-0.62	0.03		17.3	0.64		5.75	0.88	
50km x 50km												
Model with interaction												
Mean annual temperature	-0.03	0.29		-0.004	0.98		-0.17	0.98		4.5	0.60	
Annual precipitation	-0.16	0.63	0.57	-0.65	0.62	0.47	-2.8	0.97	0.35	27.5	0.73	0.65
Interaction	0.008	0.51		0.004	0.93		0.51	0.89		-0.76	0.84	
Model without interaction												
Mean annual temperature	-0.007	0.05	0.52	0.009	0.31	0.47	1.2	0.15	0.35	**2.4**	**0.01**	0.64
Annual precipitation	-0.02	0.89		**-0.58**	**0.001**		5.3	0.88		17.2	0.60	
200km x 200km												
Model with interaction												
Mean annual temperature	-0.03	0.35		-0.006	0.98		0.97	0.94		9.0	0.43	
Annual precipitation	-0.18	0.67	0.59	-0.72	0.65	0.51	-0.61	0.99	0.26	52.5	0.64	0.64
Interaction	0.009	0.57		0.006	0.94		0.006	1.0		-2.5	0.63	
Model without interaction												
Mean annual temperature	-0.007	0.10	0.52	0.01	0.64	0.51	0.98	0.96	0.26	2.3	0.07	0.60
Annual precipitation	0.01	0.95		**-0.63**	**0.04**		-0.51	0.99		16.6	0.74	

Table A5. Multiple regression results relating the magnitude of sexual dimorphism, regardless of direction, to species richness, elevation range, and their interaction in cells of different sizes. Significance was determined based on the distribution of test statistics expected under Brownian motion evolution of the response variable. All P-values are two-tailed.

	Response Variables						
	Species Richness		Elevation Range		Interaction		
Cell size	slope	P	slope	P	slope	P	R^2
100km x 100km	9×10^{-4}	0.70	7×10^{-6}	0.75	-3×10^{-7}	0.63	0.05
200km x 200km	6×10^{-4}	0.77	9×10^{-6}	0.70	-2×10^{-8}	0.66	0.06
50km x 50km	1×10^{-3}	0.59	5×10^{-6}	0.83	-4×10^{-7}	0.61	0.09

Table A6. Multiple regression results relating the magnitude of sexual dimorphism, regardless of direction, to SVL spacing, elevation range, and their interaction in cells of different sizes. Significance was determined based on the distribution of test statistics expected under Brownian motion evolution of the response variable. All P-values are two-tailed. SVL spacing was log transformed to meet regression assumptions.

	Response Variables						
	Mean SVL spacing		Elevation Range		Interaction		
Cell size	slope	P	slope	P	slope	P	R^2
100km x 100km	0.09	0.72	7×10^{-6}	0.53	-8×10^{-5}	0.39	0.02
200km x 200km	0.06	0.86	4×10^{-6}	0.76	3×10^{-7}	1.0	0.03
50km x 50km	0.10	0.75	8×10^{-6}	0.30	-1×10^{-4}	0.36	0.02

SUPPLEMENTARY MATERIAL

A biogeographic reversal in sexual size dimorphism along a continental temperature gradient

$$\bar{S} = \frac{1}{N-1}\sum_{i=1}^{N-1} s_i$$

$\bar{S}$ = mean trait spacing
s_i = SVL ratio between adjacent species in trait space
N = species richness

$$s_i = \frac{\overline{SVL_{i+1}}}{\overline{SVL_i}}$$

s_i = SVL ratio between adjacent species in trait space
$\overline{SVL_i}$ = mean snout-vent length of the i smallest species
$\overline{SVL_{i+1}}$ = mean snout-vent length of the i+1 smallest species

$$\overline{SVL} = \frac{SVL_m + SVL_f}{2}$$

$\overline{SVL}$ = species' mean snout-vent length
SVL_m = max male snout-vent length
SVL_m = max female snout-vent length

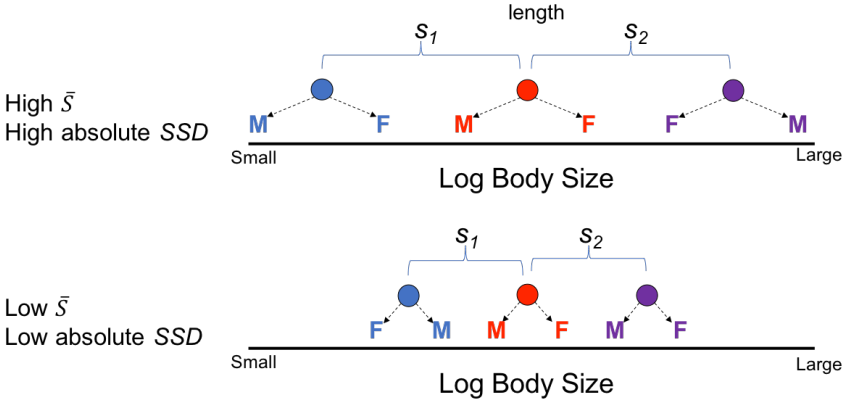

Figure A1. Body size spacing and absolute sexual size dimorphism (absolute *SSD*) under the niche divergence hypothesis. When mean body size spacing ($\bar{S}$) is high (middle panel), selection will favour high absolute *SSD* to reduce intraspecific competition. When $\bar{S}$ is low (bottom panel), absolute *SSD* is lower because interspecific competition constrains intraspecific sexual divergence. Circles indicate species' means and M and F indicate males and females, respectively. Top panel shows equations for mean trait spacing, snout-vent length (SVL) ratio among adjacent species in trait space, and the mean SVL for a species.

SUPPLEMENTARY MATERIAL

A biogeographic reversal in sexual size dimorphism along a continental temperature gradient

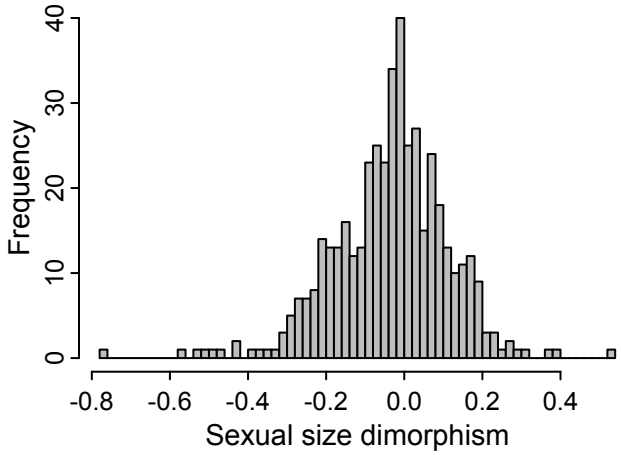

Figure A2. Distribution of sexual size dimorphism (SSD) for 446 species of lizard from North and Central America. Positive values indicate female-biased SSD and negative values male-biased SSD.

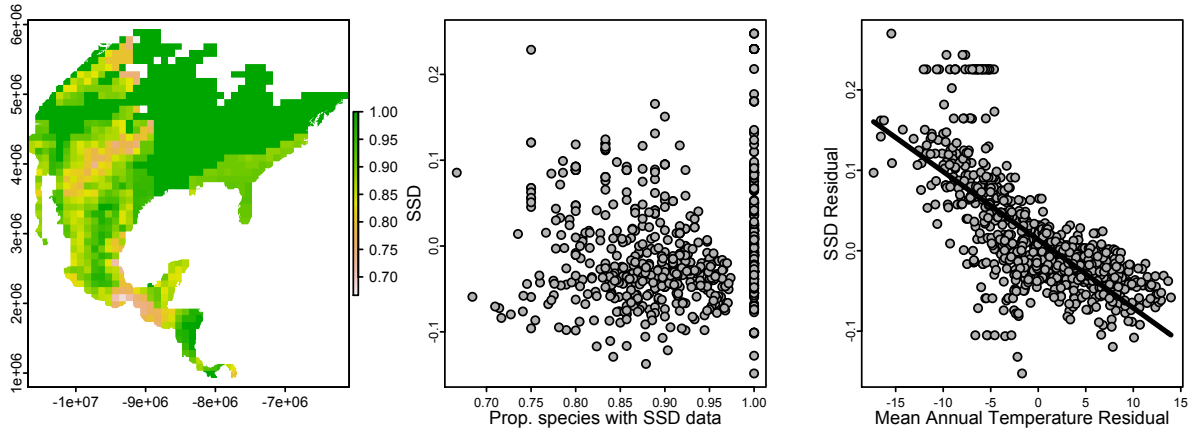

Figure A3. Variation in the proportion of species with sexual size dimorphism (SSD) data in each grid cell and its effect on the mean SSD~mean annual temperature relationship. The left panel shows the proportion of species in each grid cell with SSD data, the middle panel shows the relationship between mean SSD and the proportion of species with SSD data in each grid cell, and the right panel shows the partial regression plot of mean SSD on mean annual temperature, after accounting for the completeness of SSD data within grid cells. Specifically, in the right panel, the y-axis is the residuals from a regression of mean SSD on the proportion of species in a grid cell with SSD data and the x-axis is the residuals from a regression of mean annual temperature on the proportion of species in a grid cell with SSD data.

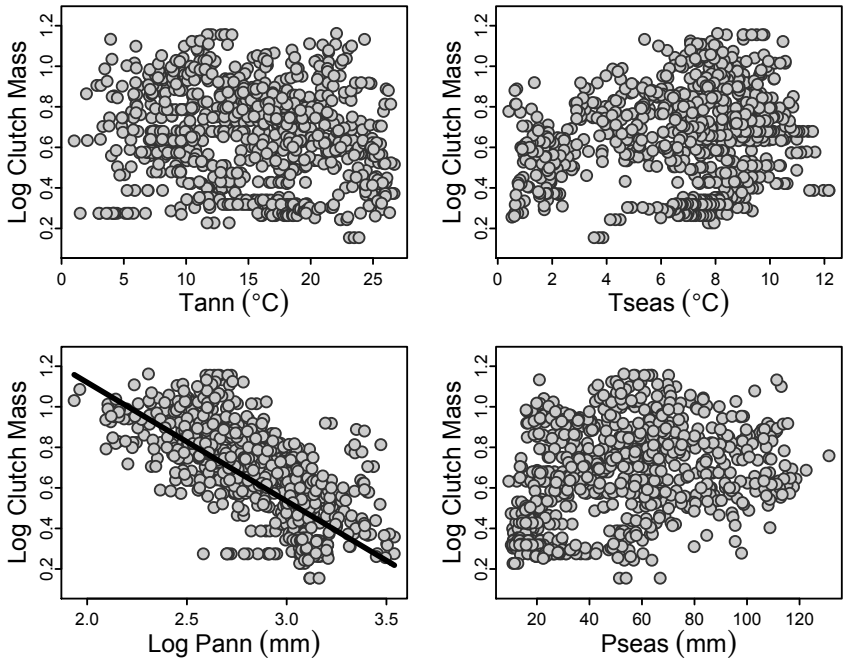

Figure A4. Relationships between mean log clutch mass and climate for lizards in 100km x 100km grid cells across North and Central America. Only the relationship with mean annual precipitation was significant (black line) relative to the expectation under Brownian motion evolution. Tann is mean annual temperature, Tseas is temperature seasonality, Pann is mean annual precipitation and Pseas is precipitation seasonality.

Table A7. List of species with range map, sexual size dimorphism (SSD) and clutch size data used in for analyses.

Species	range.map	SSD	clutch.size
Abronia anzuetoi	1	1	0
Abronia aurita	1	1	1
Abronia boqerti	1	1	0
Abronia campbelli	1	0	0
Abronia chiszari	1	1	0
Abronia cuetzpali	1	1	0
Abronia deppii	1	1	1
Abronia fimbriata	1	1	0
Abronia frosti	1	1	0
Abronia fuscolabialis	1	0	0
Abronia gaiophantasma	1	1	0
Abronia graminea	1	1	0
Abronia leurolepis	1	0	0
Abronia lythrochila	1	0	0
Abronia martindelcampoi	1	0	0
Abronia matudai	1	1	0
Abronia meledona	1	1	1
Abronia mitchelli	1	0	0
Abronia mixteca	1	0	0
Abronia montecristoi	1	0	0
Abronia oaxacae	1	0	0
Abronia ochoterenai	1	1	1
Abronia ornelasi	1	1	0
Abronia ramirezi	1	0	0
Abronia reidi	1	0	0
Abronia salvadorensis	1	0	0
Abronia smithi	1	1	0
Abronia taeniata	1	0	0
Abronia vasconcelosii	1	1	0
Ameiva ameiva	1	1	0
Anadia ocellata	1	1	0
Anadia vittata	1	0	0
Anelytropsis papillosus	1	0	0
Anniella alexanderae	1	0	0
Anniella campi	1	0	0
Anniella geronimensis	1	1	1
Anniella grinnelli	1	0	0
Anniella pulchra	1	0	1
Anniella stebbinsi	1	0	0
Anolis allisoni	1	1	0
Anolis alocomyos	1	1	0
Anolis altae	1	1	0
Anolis alvarezdeltoroi	1	1	0
Anolis amplisquamosus	1	1	0
Anolis anchicayae	1	0	0
Anolis anisolepis	1	1	0
Anolis apletophallus	1	1	0
Anolis aquaticus	1	1	0
Anolis auratus	1	1	0
Anolis barkeri	1	1	1
Anolis beckeri	1	1	0
Anolis benedikti	1	1	0
Anolis binotatus	1	0	0
Anolis biporcatus	1	1	0
Anolis boulengerianus	1	1	0
Anolis brooksi	1	1	0
Anolis campbelli	1	1	0

Anolis capito	1	1	0
Anolis carlliebi	1	1	0
Anolis carolinensis	1	1	1
Anolis carpenteri	1	1	1
Anolis casildae	1	1	0
Anolis charlesmyersi	1	1	0
Anolis chloris	1	1	0
Anolis cobanensis	1	1	0
Anolis compressicauda	1	1	0
Anolis conspersus	1	1	0
Anolis crassulus	1	1	0
Anolis cristifer	1	0	0
Anolis cryptolimifrons	1	1	0
Anolis cupreus	1	1	0
Anolis cuprinus	1	1	0
Anolis cusuco	1	1	0
Anolis cymbops	1	1	0
Anolis damulus	1	1	0
Anolis datzorum	1	1	0
Anolis dollfusianus	1	1	0
Anolis duellmani	1	1	0
Anolis dunni	1	1	0
Anolis elcopeensis	1	1	0
Anolis fortunensis	1	1	0
Anolis frenatus	1	1	0
Anolis fungosus	1	0	0
Anolis fuscoauratus	1	1	0
Anolis gadovii	1	1	0
Anolis gaigei	1	1	0
Anolis ginaelisae	1	1	0
Anolis granuliceps	1	1	0
Anolis gruuo	1	1	0
Anolis haguei	1	0	0
Anolis hobartsmithi	1	1	0
Anolis humilis	1	1	0
Anolis ibanezi	1	1	0
Anolis immaculogularis	1	1	0
Anolis insignis	1	1	0
Anolis johnmeyeri	1	1	0
Anolis kathydayae	1	1	0
Anolis kemptoni	1	1	0
Anolis kreutzi	1	1	0
Anolis kunayalae	1	1	0
Anolis laeviventris	1	1	0
Anolis latifrons	1	1	0
Anolis leditzigorum	1	1	0
Anolis lemurinus	1	1	0
Anolis limifrons	1	1	0
Anolis liogaster	1	1	0
Anolis lionotus	1	1	1
Anolis loveridgei	1	1	0
Anolis macrinii	1	1	0
Anolis macrophallus	1	1	0
Anolis maculiventris	1	1	0
Anolis magnaphallus	1	1	0
Anolis maia	1	0	0
Anolis marsupialis	1	1	0
Anolis matudai	1	1	0
Anolis mccraniei	1	1	0
Anolis megapholidotus	1	1	0
Anolis microlepidotus	1	1	0

Anolis microlepis	1	0	0
Anolis microtus	1	1	0
Anolis milleri	1	1	0
Anolis monteverde	1	1	0
Anolis morazani	1	1	0
Anolis muralla	1	1	0
Anolis naufragus	1	1	0
Anolis nebuloides	1	1	0
Anolis nebulosus	1	1	1
Anolis nietoi	1	1	0
Anolis ocelloscapularis	1	1	0
Anolis omiltemanus	1	1	0
Anolis osa	1	1	0
Anolis oxylophus	1	1	0
Anolis pachypus	1	1	0
Anolis parvicirculatus	1	1	0
Anolis pentaprion	1	1	0
Anolis petersii	1	1	0
Anolis peucephilus	1	1	0
Anolis pijolense	1	1	0
Anolis poecilopus	1	1	0
Anolis polylepis	1	1	0
Anolis pseudokemptoni	1	1	0
Anolis pseudopachypus	1	1	0
Anolis purpurescens	1	0	0
Anolis purpurgularis	1	1	0
Anolis purpuronectes	1	0	0
Anolis pygmaeus	1	0	0
Anolis quaggulus	1	1	0
Anolis quercorum	1	1	0
Anolis rodriguezii	1	1	0
Anolis rubiginosus	1	1	0
Anolis rubribarbaris	1	1	0
Anolis sacamecatensis	1	1	0
Anolis sagrei	1	1	0
Anolis salvini	1	1	0
Anolis savagei	1	0	0
Anolis schiedii	1	1	0
Anolis sericeus	1	1	0
Anolis serranoi	1	1	0
Anolis sminthus	1	1	0
Anolis spilorhipis	1	1	0
Anolis stevepoei	1	1	0
Anolis subocularis	1	1	0
Anolis taylori	1	1	0
Anolis tenorioensis	1	1	0
Anolis triumphalis	1	0	0
Anolis tropidogaster	1	1	0
Anolis tropidolepis	1	1	0
Anolis tropidonotus	1	1	0
Anolis uniformis	1	1	0
Anolis unilobatus	1	1	0
Anolis ustus	1	1	0
Anolis vittigerus	1	1	0
Anolis wampuensis	1	1	0
Anolis wellbornae	1	1	0
Anolis wermuthi	1	1	0
Anolis wilsoni	1	1	0
Anolis woodi	1	1	0
Anolis yoroensis	1	1	0
Anolis zapotecorum	1	1	0

Anolis zeus	1	1	0
Aristelliger georgeensis	1	1	0
Aspidoscelis angusticeps	1	1	0
Aspidoscelis burti	1	1	1
Aspidoscelis calidipes	1	1	0
Aspidoscelis communis	1	1	0
Aspidoscelis costatus	1	1	0
Aspidoscelis cozumela	1	0	0
Aspidoscelis deppii	1	1	0
Aspidoscelis exsanguis	1	0	0
Aspidoscelis flagellicaudus	1	0	0
Aspidoscelis gularis	1	1	1
Aspidoscelis guttatus	1	1	0
Aspidoscelis hyperythrus	1	1	0
Aspidoscelis inornatus	1	1	0
Aspidoscelis labialis	1	1	0
Aspidoscelis laredoensis	1	0	0
Aspidoscelis lineattissimus	1	1	0
Aspidoscelis marmoratus	1	1	0
Aspidoscelis maslini	1	0	0
Aspidoscelis maximus	1	1	0
Aspidoscelis mexicanus	1	1	0
Aspidoscelis motaguae	1	0	0
Aspidoscelis neomexicanus	1	0	0
Aspidoscelis neotesselatus	1	0	0
Aspidoscelis opatae	1	0	0
Aspidoscelis pai	1	1	0
Aspidoscelis parvisocius	1	1	0
Aspidoscelis rodecki	1	0	0
Aspidoscelis sackii	1	1	0
Aspidoscelis scalaris	1	1	0
Aspidoscelis sexlineatus	1	1	0
Aspidoscelis sonorae	1	0	0
Aspidoscelis stictogrammus	1	0	0
Aspidoscelis tesselatus	1	0	0
Aspidoscelis tigris	1	1	1
Aspidoscelis uniparens	1	0	0
Aspidoscelis velox	1	0	0
Aspidoscelis xanthonotus	1	0	0
Bachia blairi	1	0	0
Bachia pallidiceps	1	0	0
Barisia ciliaris	1	0	0
Barisia herrerae	1	1	1
Barisia imbricata	1	1	1
Barisia jonesi	1	0	0
Barisia levicollis	1	0	0
Barisia planifrons	1	0	0
Barisia rudicollis	1	1	1
Basiliscus basiliscus	1	1	0
Basiliscus galeritus	1	0	0
Basiliscus plumifrons	1	1	1
Basiliscus vittatus	1	1	0
Cachryx alfredschmidti	1	1	0
Cachryx defensor	1	0	0
Callisaurus draconoides	1	1	1
Celestus adercus	1	0	0
Celestus bivittatus	1	1	1
Celestus cyanochloris	1	0	0
Celestus enneagrammus	1	0	0
Celestus hylaius	1	0	0
Celestus ingridae	1	1	0

Celestus laf	1	0	0
Celestus legnotus	1	1	0
Celestus montanus	1	0	0
Celestus orobius	1	0	0
Celestus rozellae	1	0	0
Celestus scansorius	1	0	0
Cnemidophorus duellmani	1	1	0
Cnemidophorus lemniscatus	1	1	0
Cnemidophorus ruatanus	1	1	0
Coleonyx brevis	1	1	1
Coleonyx elegans	1	1	1
Coleonyx fasciatus	1	0	0
Coleonyx mitratus	1	1	1
Coleonyx reticulatus	1	1	1
Coleonyx switaki	1	0	0
Coleonyx variegatus	1	1	1
Coloptychon rhombifer	1	0	0
Copeoglossum nigropunctatum	1	1	0
Cophosaurus texanus	1	1	1
Corytophanes cristatus	1	1	0
Corytophanes hernandesii	1	0	0
Corytophanes percarinatus	1	0	0
Crotaphytus antiquus	1	1	0
Crotaphytus bicinctores	1	1	1
Crotaphytus collaris	1	1	1
Crotaphytus dickersonae	1	1	0
Crotaphytus grismeri	1	1	1
Crotaphytus insularis	1	1	0
Crotaphytus nebrius	1	1	0
Crotaphytus reticulatus	1	1	1
Crotaphytus vestigium	1	1	0
Ctenosaura acanthura	1	0	0
Ctenosaura clarki	1	1	0
Ctenosaura flavidorsalis	1	1	0
Ctenosaura hemilopha	1	1	0
Ctenosaura macrolopha	1	1	0
Ctenosaura melanosterna	1	1	1
Ctenosaura oaxacana	1	1	0
Ctenosaura palearis	1	1	0
Ctenosaura pectinata	1	1	0
Ctenosaura quinquecarinata	1	1	0
Ctenosaura similis	1	1	1
Diploglossus atitlanensis	1	0	0
Diploglossus bilobatus	1	1	1
Diploglossus monotropis	1	1	0
Diploglossus montisilvestris	1	0	0
Dipsosaurus dorsalis	1	1	1
Echinosaura horrida	1	1	0
Echinosaura palmeri	1	1	0
Echinosaura panamensis	1	1	0
Elgaria cedrosensis	1	0	0
Elgaria coerulea	1	1	1
Elgaria kingii	1	0	0
Elgaria multicarinata	1	1	1
Elgaria panamintina	1	1	0
Elgaria paucicarinata	1	1	0
Elgaria velazquezi	1	0	0
Enyalioides heterolepis	1	1	0
Gambelia copeii	1	1	0
Gambelia sila	1	1	1
Gambelia wislizenii	1	1	1

Gerrhonotus farri	1	0	0
Gerrhonotus infernalis	1	1	1
Gerrhonotus lazcanoi	1	0	0
Gerrhonotus liocephalus	1	1	0
Gerrhonotus lugoi	1	0	0
Gerrhonotus ophiurus	1	1	0
Gerrhonotus parvus	1	0	0
Gonatodes albogularis	1	1	0
Gymnophthalmus speciosus	1	1	0
Heloderma horridum	1	1	1
Heloderma suspectum	1	1	1
Holbrookia approximans	1	1	0
Holbrookia elegans	1	1	0
Holbrookia lacerata	1	0	0
Holbrookia maculata	1	1	1
Holbrookia propinqua	1	1	1
Holcosus anomalus	1	1	0
Holcosus chaitzami	1	1	0
Holcosus festivus	1	1	0
Holcosus leptophrys	1	1	0
Holcosus quadrilineatus	1	1	1
Holcosus undulatus	1	1	1
Iguana iguana	1	1	0
Laemanctus longipes	1	1	1
Laemanctus serratus	1	0	0
Lepidoblepharis emberawoundule	1	0	0
Lepidoblepharis rufigularis	1	0	0
Lepidoblepharis sanctaemartae	1	0	0
Lepidoblepharis victormartinezi	1	0	0
Lepidoblepharis xanthostigma	1	1	0
Lepidophyma chicoasensis	1	0	0
Lepidophyma cuicateca	1	0	0
Lepidophyma dontomasi	1	1	0
Lepidophyma flavimaculatum	1	1	1
Lepidophyma gaigeae	1	1	0
Lepidophyma lineri	1	0	0
Lepidophyma lipetzi	1	0	0
Lepidophyma lowei	1	0	0
Lepidophyma mayae	1	0	0
Lepidophyma micropholis	1	1	0
Lepidophyma occulor	1	1	0
Lepidophyma pajapanensis	1	0	0
Lepidophyma radula	1	0	0
Lepidophyma reticulatum	1	0	0
Lepidophyma smithii	1	0	0
Lepidophyma sylvaticum	1	1	0
Lepidophyma tarascae	1	1	0
Lepidophyma tuxtlae	1	1	0
Lepidophyma zongolica	1	0	0
Loxopholis rugiceps	1	1	0
Loxopholis southi	1	1	0
Marisora alliacea	1	1	0
Marisora brachypoda	1	1	0
Marisora unimarginata	1	1	0
Mesaspis antauges	1	1	0
Mesaspis cuchumatanus	1	1	0
Mesaspis gadovii	1	1	1
Mesaspis juarezi	1	1	1
Mesaspis monticola	1	1	1
Mesaspis moreletii	1	1	1
Mesaspis viridiflava	1	0	0

Mesoscincus altamirani	1	1	0
Mesoscincus managuae	1	0	0
Mesoscincus schwartzei	1	1	0
Morunasaurus groi	1	1	0
Ophisaurus attenuatus	1	1	1
Ophisaurus ceroni	1	0	0
Ophisaurus compressus	1	1	1
Ophisaurus incomptus	1	0	0
Ophisaurus mimicus	1	1	0
Ophisaurus ventralis	1	0	0
Petrosaurus mearnsi	1	0	0
Petrosaurus repens	1	0	0
Petrosaurus thalassinus	1	1	0
Pholidobolus vertebralis	1	1	0
Phrynosoma asio	1	0	0
Phrynosoma bauri	1	1	0
Phrynosoma blainvillii	1	1	0
Phrynosoma braconnieri	1	1	0
Phrynosoma brevirostris	1	1	0
Phrynosoma cerroense	1	1	0
Phrynosoma cornutum	1	1	1
Phrynosoma coronatum	1	1	1
Phrynosoma diminutum	1	1	0
Phrynosoma ditmarsi	1	1	1
Phrynosoma douglasii	1	0	1
Phrynosoma goodei	1	0	0
Phrynosoma hernandesi	1	1	1
Phrynosoma mcallii	1	1	1
Phrynosoma modestum	1	1	1
Phrynosoma orbiculare	1	1	0
Phrynosoma ornatissimum	1	0	0
Phrynosoma platyrhinos	1	1	1
Phrynosoma sherbrookei	1	1	0
Phrynosoma solare	1	1	1
Phrynosoma taurus	1	1	0
Phyllodactylus bordai	1	1	0
Phyllodactylus davisi	1	0	0
Phyllodactylus delcampoi	1	0	0
Phyllodactylus duellmani	1	0	0
Phyllodactylus homolepidurus	1	0	0
Phyllodactylus lanei	1	1	1
Phyllodactylus muralis	1	1	0
Phyllodactylus nocticolus	1	1	0
Phyllodactylus papenfussi	1	0	0
Phyllodactylus paucituberculatus	1	0	0
Phyllodactylus tuberculosus	1	1	1
Phyllodactylus unctus	1	1	0
Phyllodactylus xanti	1	1	0
Plestiodon anthracinus	1	1	1
Plestiodon bilineatus	1	0	0
Plestiodon brevirostris	1	1	0
Plestiodon callicephalus	1	1	0
Plestiodon colimensis	1	0	0
Plestiodon copei	1	1	1
Plestiodon dicei	1	0	0
Plestiodon dugesii	1	1	0
Plestiodon egregius	1	1	1
Plestiodon fasciatus	1	1	1
Plestiodon gilberti	1	1	1
Plestiodon indubitus	1	1	0
Plestiodon inexpectatus	1	1	1

Plestiodon lagunensis	1	1	0
Plestiodon laticeps	1	1	1
Plestiodon lotus	1	0	0
Plestiodon lynxe	1	1	1
Plestiodon multilineatus	1	0	0
Plestiodon multivirgatus	1	1	1
Plestiodon nietoi	1	0	0
Plestiodon obsoletus	1	1	1
Plestiodon ochoterenae	1	1	0
Plestiodon parviauriculatus	1	1	1
Plestiodon parvulus	1	0	0
Plestiodon reynoldsi	1	1	0
Plestiodon septentrionalis	1	1	1
Plestiodon skiltonianus	1	1	1
Plestiodon sumichrasti	1	1	1
Plestiodon tetragrammus	1	1	1
Polychrus gutturosus	1	1	0
Polychrus marmoratus	1	1	0
Potamites apodemus	1	1	0
Ptychoglossus festae	1	1	0
Ptychoglossus myersi	1	1	0
Ptychoglossus plicatus	1	1	0
Sauromalus ater	1	1	1
Sauromalus hispidus	1	1	0
Sauromalus varius	1	1	0
Sceloporus acanthinus	1	0	0
Sceloporus adleri	1	1	0
Sceloporus aeneus	1	1	1
Sceloporus albiventris	1	0	0
Sceloporus anahuacus	1	0	0
Sceloporus arenicolus	1	1	0
Sceloporus asper	1	0	0
Sceloporus aurantius	1	0	0
Sceloporus aureolus	1	1	0
Sceloporus bicanthalis	1	1	1
Sceloporus bimaculosus	1	1	0
Sceloporus brownorum	1	1	0
Sceloporus bulleri	1	1	0
Sceloporus caeruleus	1	0	0
Sceloporus carinatus	1	0	0
Sceloporus cautus	1	1	0
Sceloporus chaneyi	1	0	0
Sceloporus chrysostictus	1	1	1
Sceloporus clarkii	1	1	1
Sceloporus consobrinus	1	1	0
Sceloporus couchii	1	1	0
Sceloporus cowlesi	1	1	0
Sceloporus cozumelae	1	1	1
Sceloporus cryptus	1	1	0
Sceloporus cupreus	1	0	0
Sceloporus cyanogenys	1	1	0
Sceloporus cyanostictus	1	1	0
Sceloporus druckercolini	1	0	0
Sceloporus dugesii	1	1	1
Sceloporus edbelli	1	1	0
Sceloporus edwardtaylori	1	0	0
Sceloporus exsul	1	0	0
Sceloporus formosus	1	1	1
Sceloporus gadoviae	1	1	1
Sceloporus gadsdeni	1	1	0
Sceloporus goldmani	1	1	0

Sceloporus graciosus	1	1	1
Sceloporus grammicus	1	1	1
Sceloporus grandaevus	1	1	0
Sceloporus halli	1	0	0
Sceloporus heterolepis	1	1	0
Sceloporus horridus	1	1	1
Sceloporus hunsakeri	1	1	0
Sceloporus insignis	1	1	0
Sceloporus internasalis	1	0	0
Sceloporus jalapae	1	1	1
Sceloporus jarrovii	1	1	0
Sceloporus lemosespinali	1	1	0
Sceloporus licki	1	0	0
Sceloporus lunae	1	0	0
Sceloporus lundelli	1	1	0
Sceloporus macdougalli	1	1	0
Sceloporus maculosus	1	0	0
Sceloporus magister	1	1	1
Sceloporus malachiticus	1	1	1
Sceloporus megalepidurus	1	1	0
Sceloporus melanorhinus	1	1	0
Sceloporus merriami	1	1	1
Sceloporus minor	1	1	0
Sceloporus mucronatus	1	1	1
Sceloporus nelsoni	1	1	0
Sceloporus oberon	1	1	0
Sceloporus occidentalis	1	1	1
Sceloporus ochoterenae	1	1	1
Sceloporus olivaceus	1	1	1
Sceloporus omiltemanus	1	1	0
Sceloporus orcutti	1	1	1
Sceloporus ornatus	1	1	0
Sceloporus palaciosi	1	1	0
Sceloporus parvus	1	1	0
Sceloporus poinsettii	1	1	1
Sceloporus pyrocephalus	1	1	1
Sceloporus salvini	1	0	0
Sceloporus samcolemani	1	1	0
Sceloporus scalaris	1	1	1
Sceloporus serrifer	1	0	0
Sceloporus shannonorum	1	1	0
Sceloporus siniferus	1	1	1
Sceloporus slevini	1	1	0
Sceloporus smaragdinus	1	1	0
Sceloporus smithi	1	0	0
Sceloporus spinosus	1	1	1
Sceloporus squamosus	1	1	0
Sceloporus stejnegeri	1	1	0
Sceloporus subpictus	1	1	0
Sceloporus sugillatus	1	1	0
Sceloporus taeniocnemis	1	1	0
Sceloporus tanneri	1	0	0
Sceloporus teapensis	1	1	0
Sceloporus torquatus	1	1	1
Sceloporus tristichus	1	1	0
Sceloporus undulatus	1	1	1
Sceloporus unicanthalis	1	0	0
Sceloporus uniformis	1	1	0
Sceloporus utiformis	1	1	1
Sceloporus variabilis	1	1	1
Sceloporus virgatus	1	1	1

Sceloporus woodi	1	1	1
Sceloporus zosteromus	1	1	1
Scincella assatus	1	0	0
Scincella caudaequinae	1	1	0
Scincella cherriei	1	1	0
Scincella forbesora	1	1	0
Scincella gemmingeri	1	1	0
Scincella incerta	1	0	0
Scincella kikaapoa	1	0	0
Scincella lateralis	1	1	1
Scincella silvicola	1	1	1
Sphaerodactylus argus	1	1	0
Sphaerodactylus continentalis	1	0	0
Sphaerodactylus dunni	1	0	0
Sphaerodactylus glaucus	1	1	1
Sphaerodactylus graptolaemus	1	1	0
Sphaerodactylus homolepis	1	1	1
Sphaerodactylus lineolatus	1	1	0
Sphaerodactylus millepunctatus	1	1	1
Sphaerodactylus notatus	1	1	0
Sphenomorphus rarus	1	0	0
Thecadactylus rapicauda	1	1	0
Tretioscincus bifasciatus	1	0	0
Tupinambis teguixin	1	1	0
Uma cowlesi	1	1	0
Uma exsul	1	1	1
Uma inornata	1	1	0
Uma notata	1	1	1
Uma paraphygas	1	1	1
Uma scoparia	1	1	1
Urosaurus bicarinatus	1	1	1
Urosaurus gadovi	1	1	0
Urosaurus graciosus	1	1	1
Urosaurus lahtelai	1	0	0
Urosaurus nigricaudus	1	1	0
Urosaurus ornatus	1	1	1
Uta stansburiana	1	1	1
Xantusia arizonae	1	1	1
Xantusia bezyi	1	1	0
Xantusia bolsonae	1	1	1
Xantusia extorris	1	1	1
Xantusia gilberti	1	0	0
Xantusia gracilis	1	0	0
Xantusia henshawi	1	1	1
Xantusia jaycolei	1	0	0
Xantusia sanchezi	1	1	1
Xantusia sherbrookei	1	0	0
Xantusia sierrae	1	1	0
Xantusia vigilis	1	1	1
Xantusia wigginsi	1	1	0
Xenosaurus agrenon	1	0	0
Xenosaurus arboreus	1	0	0
Xenosaurus grandis	1	1	1
Xenosaurus mendozai	1	1	0
Xenosaurus newmanorum	1	1	1
Xenosaurus penai	1	1	0
Xenosaurus phalaroanthereon	1	0	0
Xenosaurus platyceps	1	1	1
Xenosaurus rackhami	1	0	0
Xenosaurus rectocollaris	1	1	1
Xenosaurus tzacualtipantecus	1	0	0

SUPPLEMENTARY MATERIAL

A biogeographic reversal in sexual size dimorphism along a continental temperature gradient